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Founded in 1845, the *Koninklijke Nederlandsche Botanische Vereeniging* (Royal Botanical Society of the Netherlands) has represented, through its members, the study of botanical science in the Netherlands for more than a century.

Up to the present time two journals have been published under the auspices of the society, namely the "Nederlandsch Kruidkundig Archief", firstly in 1846, which dealt mainly with Dutch flora and plant taxonomy and was written in Dutch and the "Recueil des Travaux Botaniques Néerlandais", published in 1904. The articles in this journal were written in English, German or French and while being concerned with all branches in botanical science, particular emphasis was laid upon experimental botany.

From January 1952 both journals will be replaced by the *Acta Botanica Neerlandica*, of which almost all articles will be in English, French or German. This journal will cover the work of member botanists in their different branches, performed in Holland, in the tropics or elsewhere. The varied nature of the articles must prove of particular value to all botanists in this era of overspecialisation.

The board of editors of the new journal will be constituted a.o. by the directors of the botanical laboratories in the universities of Amsterdam (VAN HERK and HEIMANS); Delft (ROELOFSEN); Groningen (ARISZ); Leiden (VAN DEN HONERT); Utrecht (KONINGSBERGER and LANJOUW); Wageningen (WASSINK), of the Laboratory for Flowerbulb Research at Lisse (VAN SLOGTEREN), and the Phytopathological Laboratory "Willie Commelin Scholten" at Baarn (WESTERDIJK), with a few specialists in different fields.

The journal will appear quarterly and come to a volume of about 500 pages per annum.

We sincerely hope that the *Acta Botanica Neerlandica* may further the cooperation and friendship of botanists in the Netherlands with their colleagues the world over.

Lisse, January 1952

VAN SLOGTEREN
President of the Koninklijke Nederlandsche
Botanische Vereeniging

THE GENUS ORTHODONTIUM

BY

W. MEIJER

Received October 3, 1951

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Chapter I

INTRODUCTION

1. The present state of taxonomic bryology

At the present day scientists pay relatively little attention to the taxonomy of cryptogams, especially when it concerns such groups with little practical importance as the bryophytes.

Thus we see that special branches of biology are developed in minute details, while others are more neglected than is justified from a purely scientific point of view.

Bryophytes provide most interesting illustrations of morphological phenomena. They offer in their distribution many traits which are valuable in the field of bio-geography. They help us to demonstrate the richness of life, the course of evolution. And there is even a practical side of this part of science, for field knowledge of bryophytes helps us to trace the differences in micro- en general climate and the differences in the composition of soils and rocks.

We should not passively accept the fact of the deplorable state of present day taxonomic bryology. When we develop first of all the systematics of this group, explorations of a wider perspective will be possible. At present the bulk of the work of bryologists consists in naming collections from different parts of the world, giving lists of the new finds and describing new species. It is obvious that only a well trained specialist can do this work with fairly satisfactory result.

But we should earnestly take into consideration the question whether it would not be better to devote more time to elucidate the taxonomy of special groups instead of trying to publish the names of all specimens of new collections.

Bryological floras of great parts of the world are still lacking. Verdoorn (1950) gave a vivid description of the hopeless condition of a botanist in a tropical region, trying to determinate the species collected, even in the neighbourhood of a well equipped botanical institute.

We lack moss floras of South America and of Africa. Outside the well studied European and North American regions we only possess a critical moss flora of Java and surrounding regions by Fleischer (1922), one of the Philippines by Bartram (1939) and from Middle America one of Guatemala by the same author. Moss floras of Tasmania, New Zealand and Australia are quite out of date. The only complete worldwide survey of the moss genera is that by Brotherus (1909) in Engler and Prantl's "Natürliche Pflanzenfamilien". This work is only a tentative survey, by one of the bryologists who were shifting and naming collections of all parts of the world, during their lifetime.

It is becoming obvious to most bryologists that we are handicapped by a great burden of superfluous species names, caused by the lack of coordination in former days.

As Verdoorn (1945) stated: "The terrible status of exotic cryptogamic taxonomy cries for some kind of concentrated attack".

We lack special foundations, special publishing opportunities, as well as stimulation centers, like the former Annales Bryologici and Hedwigia. Few bryologists are working in special cryptogamic departments of greater botanical institutes. The revision work which has been done during the last four decennia, notwithstanding the difficult circumstances show how much can be done in this field.

The last monograph on a moss genus was Malta's: "Die Gattung *Zygodon* (1926)". It was shown by this excellent treatise of a genus that approximately half of the c. 160 species names were superfluous.

Other examples are the work done by Verdoorn, Herzog and his pupils in Malayan hepatics, by FULFORD in the genus *Bazzania* from South America. Still the words of FLEISCHER (1922) are right when he called monographic work: "die grosse und zugleich auch wichtigste Zukunftsaufgabe der systematischen Bryologie".

2. THE PROBLEM OF NARROWLY RELATED SPECIES

The rapid increase of the number of named species forms a danger for scientific taxonomy in bryophytes. We may not overlook the fact that among bryophytes as in other groups there may exist narrowly related species which can be hardly recognized on a morphological basis, but which have to be considered as separate species. Recent examples of such concealed species from the thoroughly studied European moss floras are *Calliergon megalophyllum* and *Drepanocladus tundrae*, which we have learned to distinguish by the aid of TUOMIKOSKI (1940, 1949).

In this way from time to time we will detect that some narrowly limited species have to be maintained as being separate, because they really behave as such, e.g. by growing together in the same habitat.

These phenomena are less amazing when we bear in mind the results of recent cytogenetical and cytotaxonomical investigations, revealing that one of the causes of species formation is sexual isolation following genetic changes. If we try to explain the taxonomic value of narrowly related species, occurring in the same ecological niche, considerations of that kind cannot be omitted.

3. THE APPLICATION OF GENETIC CONCEPTS IN BRYOLOGY

Until now genetical concepts are often neglected in bryological taxonomy. The following words of VERDOORN (1934) are still applicable here: "Fragen wir uns welche Änderungen die Genetik im Artproblem im Allgemeinen hervorgerufen hat und überlegen dann, ob alle diese Tatsachen, Schlüsse und Hypothesen einen direkten Einfluss auf die Bryologie ausgeübt haben, so finden wir von all dem kaum eine Spur".

In Phanerogamic and Zoological taxonomy these genetic concepts have given much useful explanation, a fruitful use of new terms as 'geographic and ecological subspecies', a better evaluation and investigation of hybrid forms and a theoretical justification of a more general use of a broad species concept (Reviews in E. MAYER 1942, HUXLEY 1940, STEBBINS 1950).

We have a strong suspicion that the same regularities are playing a role among bryophytes, but we are still working too much on orthodox lines, without recognizing subspecies where we certainly have a right to establish them, neglecting the fact that most species are genetically polymorphous and we are unconscious of the possibility that we are dealing partly with hybrid forms.

It is true that we need more experimental work in bryophytes before we can apply terms and concepts which have proved their usefulness in groups studied by experimental methods. But certain extrapolations seem justified. For example, in the present study *Orthodontium brevicollum* Fleischer, a form which lives on the mountains of Java and Ceylon, in the same habitats as *O. infractum* Dozy & Molkenboer, is no longer considered as a subspecies of the last species. In my opinion we should either treat it as a separate species or as a minor variant.

Among well known European mosses *Eurhynchium striatum* offers a beautiful example of a species divided in geographical subspecies.

This pleurocarp moss is common in our woods. PÉR STØRMER (1942) described a form of this species with more cordate-ovate leaves as a new species: *E. zetterstedtii.* The type of *E. striatum* s.str. possesses acuminate leaves. STØRMER was able to point out that the acuminate type (*E. striatum* s.str.) has a more western distribution in Norway, than the cordate-ovate (*E. zetterstedtii*). Most of the localities of *E. striatum* on the continent of Europe are situated west of a line from Hamburg to Zürich and those of *E. zetterstedtii* occur east of this line. In our opinion this case is quite parallel with that of geographical subspecies among birds and among phanerogams. Therefore it would be more in accordance with modern investigations to call both forms subspecies of *E. striatum* (Hedw.) Schimp.

Until recently so narrow a species concept has been used by European bryologists that differences between species are often considered to consist only of one constant elementary character. In such a way the hepatic *Calypogeia trichomanis* (L) Corda was considered by most hepaticologists as distinguished from *Calypogeia mülleriana*, because the former possesses blue oil bodies in the cells and the latter translucent ones.[1] The latter form seems to possess a more continental distribution. By my own studies of the genus *Riccia* and of *Lophozia* I am convinced that in such genera the minor species certainly can be arranged in several polytypic major species.

As to the possibility of hybridization, in studying the genus Orthodontium, my suspicion has been raised that in a special part of its range the wide variation of forms is partly caused by hybridization. This possibility has never been taken into consideration. As a matter of fact it is very difficult to recognize derivatives of moss hybrids as such and to distinguish them from aberrant forms with only slight variation, caused by mutation (LOTSY, 1928). We may safely accept that hybrids occur among mosses as well as among phanerogams. For further details on this subject we refer to chapter III.

It is obvious that such phenomena are apt to cause great difficulties when we try to draw lines of demarcation between the taxa, in the same way as in some difficult groups of phanerogams.

Matters become even more complicated when the plants are monoecious as in Orthodontium. Then each variant of a variable population may show a certain autonomy, because whole tufts of a special habit can be formed from one single spore. Selffertilisation takes place then and causes the same form with the same habit to be distributed in the neighbourhood. In this way different pure lines next to each other may have come into existence in the same area. Sexual isolation between these forms is only temporarily maintained, until two different forms come to grow intermingled in one tuft. Only twice I found two forms growing intermixed. The consequence of this relation of the sexes and this way of growing is that within each species a high polymorphism may exist and that the demarcation between species and subspecies is rather vague.

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[1] LINNAEUS must apparently have dealt with the form with translucent oil bodies, because the other is very rare in Sweden, occurring only in the extreme South (ARNELL, in litt.). Thus from a nomenclatorial point of view the names are also wroug.

All this makes the taxonomy of these groups very difficult.

Chapter II

HISTORY OF THE GENUS

1. The period of 1827—1850

Schwaegrichen (1827) described for the first time the genus Orthodontium in the family Bryaceae. It has a double peristome of characteristic construction, not as fully developed as the peristome of *Bryum* and *Pohlia* and quite typical in its teeth, which are straight and erect when moistened, whence the name Orthodontium.

The genus was founded on *O. julaceum* and *O. lineare*, the first of which was afterwards placed in Bryum, section *Cladodium*, by Bruch & Schimper (1844). Ten years afterwards (1837) W. J. Hooker published in his Icones Plantarum a new species, *Bryum pellucens*, correctly placed in Orthodontium by Bruch & Schimper (1844). *Orthodontium pellucens* (Hooker) Br. et Schimp. had been found by Jameson, near Quenca in Colombia (S. America).

It is interesting to note that Hooker (1837) in the notes following the description of *Bryum pellucens* calls attention to a new find of Orthodontium by his English colleague Wilson:

"It is not a little remarkable that about the same time that Professor Jameson found this beautiful and delicate moss in South America, Mr. W. Wilson detected a species of the same genus in England, so much resembling it that, except its smaller size, narrower and more subulate and not at all glossy leaves, is it hardly to be distinguished from it: *Bryum gracile* Wils. in Gardn. Musc. Brit. t. 34 App. (1839)".

In these words two of the most important differences are indicated between the South American *O. pellucens* and the British *Bryum gracile*, afterwards called *Orthodontium gracile* by Bruch and Schimper, viz. smaller leaves, not at all glossy. The minor differences in the peristomes were not observed.

This is possibly one of the reasons why Wilson at first did not think his *Bryum gracile* to be different from *Orthodontium lineare*. He preferred however to place *O. lineare* in the genus *Bryum*, but he had to choose then a new specific epithet, because the name *Bryum lineare* was in use already. He thus gave *Orthodontium lineare* as a synonym of *Bryum gracile*.

Bruch and Schimper (lit. c.) were the first who dealt with the South African and the European plants as two different species, placed in the genus Orthodontium, together with the South American *O. pellucens* (Hook.) Br. et Schimp. Wilson cited in his herbarium the name *Orthodontium gracile* Schwaegr. Schwaegrichen wrote to him, according to Bruch and Schimper (1844), that in his opinion *Bryum gracile* and *O. lineare* were different. In this connection it is interesting to make a careful study of Wilson's fine herbarium sheets (in the herbarium of the British Museum, London), fully illustrated with beautiful drawings and long annotations. Wilson was at first inclined to consider all the three forms together as representatives of *O. lineare*, but afterwards he changed his opinion and we read: "Surrucucho, Jameson, a specimen of *O. pellucens*, is perhaps *O. lineare* Schwaegr.", but he wrote on the annotation: "Differs from *O. lineare* Schwaegr." and he pointed out some differences: "Leaves not so narrow, opercule longer".

As will be shown later these differences will stand the closest examination.

From the fact that in a more recent sheet in Wilson's herbarium we read "*Orthodontium gracile* Schwaegr., Helsby (Cheshire) 1844", instead of "*Bryum gracile*", we can conclude that Wilson afterwards agreed that the English Orthodontium was distinct from *O. lineare* Schwaegr. He also investigated another important difference: "This has antheridia with paraphyses in the axils of the perichaetial leaves, unlike what is recorded by Schwaegr. (1827) of *O. lineare*, which has terminal male flowers with ovate perigonal leaves". That Wilson had still not seen the original specimen of *O. lineare* and was therefore always somewhat uncertain of its real position, appears from the following. During an expedition into the southern circumpolar regions (1830—1843), Tasmania and New Zealand in H.M. Ships Erebus and Terror, J. D. Hooker, the son of W. J. Hooker, collected another Orthodontium in the Falkland Islands, at Hermite Island and in Tasmania. This find was apparently also very carefully studied by Wilson. He pointed out clearly the differences from *Orthodontium gracile*, but wrote in a note on a herbarium sheet: "*O. australe* mihi, *O. lineare* Schwaegr?". It should be stated here that the differences between *O. australe* and *O. lineare* are indeed rather slight (see chapter III).

The collections from Hermite Island and the Falkland Islands were also carefully compared with *O. gracile* from Helsby. Among the differences the most outstanding are the following: "sporular sac extending nearly 3/4 of the whole length, of thicker texture, somewhat furrowed when dry. Generally, the outer peristome teeth shorter than the inner, the segments with a central line, leaf nerve more defined. Seta generally longer".

Up till then the study of Orthodontium by well known bryologists such as Wilson, J. D. Hooker, Bruch and Schimper had been based on careful study and a broad species concept. In most cases the real differences between the forms studied were described. It was however a misfortune that so little of the type species of the genus, *O. lineare*, had been gathered, that Wilson and Hooker had no material for comparison and had always to rely upon Schwaegrichen's description and figure. Another unfortunate fact was that most collections of *O. australe* had young sporogonia which differ from old ones in the very smooth capsules. The same was true of the type specimen of *O. lineare*, as Schwaegrichen also had before him a specimen with young smooth capsules. Now we know that in both species old capsules can be distinctly furrowed, but in those days they were considered to be smooth or only somewhat furrowed, and this was accepted as an important character. When afterwards James Drummond sent a specimen from Australia of an Orthodontium with distinct furrowed capsules, it was described by Hooker fil. and Wilson (1848) as *O. sulcatum*. A further disadvantage was that out of the whole form complex in Australia, to which this *O. sulcatum* belongs, just this variant, with extremely broad leaves, had been selected for the first description. Thus Hooker and Wilson wrote (1848): "Allied to *O. lineare* Schwaegr., but different essentially from that and other species in the furrowed capsule. The leaves are shorter and not gradually tapering".

The consequence of this was that forms from Australia, differing from this type, were described as new species, with no possibility of sharp demarcation, e.g. *O. lanceolatum* Mitten 1856 (now to be considered as a 'small' form of *O. sulcatum*) and *O. zetterstedtii* C.M. 1898. I still cannot understand why C. Müller (Halle) described the latter as a new species. Yet it is a curious fact that we find in the herbaria of Hooker and Wilson specimens from New Holland labelled *Orthodontium lineare*.

This raises the question whether *O. lineare* really occurs in Australia and what is its relation to *O. sulcatum*.

The collections of Hooker and Wilson were too few to allow a satisfactory classification of this very puzzling and complicate Australian-Subantarctic form complex.

Meanwhile a distinct, more isolated species of the genus was described from Malesia by Dozy and Molkenboer (1844): *O. infractum*. Till that date only *O. lineare*, *O. gracile* and *O. pellucens* had been described. Dozy and Molkenboer (1844) had made use of the Bryologia Europaea, but they had not yet seen Hooker and Wilson's description of *O. australe*. They pointed out that as to the distribution of antheridia and archegonia *O. infractum* is similar to *O. lineare*, but differs in length and form of the lid. The differences in the peristome from *O. pellucens* are of great importance. The initial stage in the taxonomy of the genus Orthodontium, which occupied the first half of the 19th century, was thus critical and thoughtful.

2. The period between 1850—1900

Now followed a period during which the creation of new species on a large scale seemed to be the fashion, it is the period of the famous geographical method, by which new finds from different parts of the world were too readily described as new species, without sufficient painstaking investigation. Of course there were some exceptions, but on the whole most superfluous species of Orthodontium were described between 1850 and 1900:

1855, *O. aethiopicum* C.M.; 1856, *O. lanceolatum* Mitten; 1857, *O. osculatianum* De Not.; 1860, *O. setaceum* W. P. Schimper, nom. nud.; 1865, *O. confine* Hpe; 1869, *O. tenellum* Mitten; 1878, *O. fendleri* Hpe; 1893, *O. ovale* C.M. in litt. ad Broth.; 1898, *O. arenarium* C.M.; 1898, *O. ulei* C.M.; 1898, *O. zetterstedtii* C.M. and 1898, *O. laxirete* Dusen, nom. nud.

On the average, two superfluous species of Orthodontium have been described every ten years during this period. Three by Hampe, four by C. Müller and two by Mitten, who was the most critical of the above named workers.

We have seen already that his *O. lanceolatum* at first sight comprises a form with narrower leaves than *O. sulcatum*. But from his herbarium we do not get a uniform picture of the species created (see chapter III). He compared his *O. lanceolatum* especially with *O. australe*.

O. tenellum also has at first sight a somewhat different aspect from *O. gracile*, with which it was afterwards joined by Le Roy Andrews, in our opinion on good grounds.

The other species created during the geographical period, indicated above, are so clearly identical with species previously described that we shall pay no more attention to them for the present. C. Müller and Hampe as well as Mitten however had among their creations some really new forms which deserve to be called separate species:

1880—1881, *O. loreifolium* Besch.; 1881, *O. denticulatum* Geheeb & Hampe; 1885, *Apalodium inflatum* Mitten, and 1863, *O. longisetum* Hampe.

The first two are very closely related to *O. pellucens* and are probably derived from this species. The same may be true of *O. loreifolium* Besch. (1880—1881). *Orthodontium inflatum* (Mitten) is an Australian species, probably related to *O. infractum* Dozy & Molkenb.

3. Subdivision of the genus

In the meantime some attempts were made to split the genus Orthodontium. Mitten (1869) did this in a rather curious way. He separated the genus Apalodium (with *A. pellucens* and *A. australe*) from Orthodontium sensu stricto (with *O. tenellum* and *O. gracile*) and placed the former in the family Orthotrichaceae. Consequently (as was clear from his publication of 1885) the type species of the genus

Orthodontium, *O. lineare*, had been put by Mitten (1869) in Apalodium, contrary to the rules of nomenclature, as these are accepted today.

Mitten (1885) wrote on p. 198: "*Apalodium lineare*, Schwaegr. t. 188 (Orthodontium), from South Africa, is described and figured with the inner and outer peristome equal in length".

In the meantime Lindberg (1878) accepted Mitten's view that *O. gracile* stood sufficiently apart to justify the formation of a genus, containing this species and separate from the other species of Orthodontium. He put things in order when he rejected Mitten's name Apalodium and created for *O. gracile* a separate genus Stableria. His arguments run as follows:

O. lineare Schwaegr. is the first representative of a separate genus. It belongs to the same group which has been called Apalodium by Mitten (1869). Then Lindberg (1878) continues in the following words: "the conclusion from this is that both Orthodontium and Apalodium are synonymous. The European species *O. gracile* has nothing to do with this genus Orthodontium: it belongs to quite a different family and has not any analogy with it. Because it forms thus a distinct separate genus, we feel ourselves obliged to give it another genus name, choosing the name Stableria, after our good friend, the late Mr. G. Stabler, from Westmoreland" (translated by the author).

It is curious to note that Mitten (1869) as well as Lindberg (1878) gave no details of what in their opinion were the differences between Orthodontium and Stableria. It seems somewhat strange that they both considered the genera Orthodontium and Stableria to belong to two different families:

1. Orthotrichaceae: Apalodium Mitten = Orthodontium Schwaegr.
2. Bryaceae: Orthodontium Mitten = Stableria Lindb.

Brotherus (1909) maintained Stableria as well as Orthodontium and placed both genera in a subfamily of the family Bryaceae. In our opinion they are there in the right position.

Reimers (1941) and following him Margadant & Meijer (1950), suggested that the creation of Stableria by Mitten has been caused by a systematic error of Lindberg:

"Offenbar verhält es sich so, dass Mitten eine der tropischen Orthodontium-Arten versehentlich als *Apalodium lineare* zu den Orthotrichaceae stellte und S. O. Lindberg, in der Meinung dass diese Umstellung der Typusart *Orthodontium lineare* galt, für das von ihm als Bryaceae erkannte europäische *O. gracile* den neuen Gattungsnamen Stableria bildete".

In our opinion however Lindberg was right when he considered Apalodium synonymous with Orthodontium Schwaegr., when reading Mitten's paper of 1869, and it was quite logical that his taxonomic concept of the whole genus induced the creation of Stableria.

Matters are still more obscured by the fact that Mitten used the name *Apalodium lineare*, in a paper of 1883 as a synonym of *Weissia* *pallens* Hook. & Wils. 1848 and of *Zygodon lineare* Taylor nom. nud. The last name we find also in MITTEN's herbarium on the type sheet of *Orthodontium pallens* (Hook. & Wils.) Broth.

Thus MITTEN's name *Apalodium lineare* (Schwaegr.) Mitten 1885 is a later homonym of *A. lineare* (Taylor) Mitten 1883, and in some herbaria specimens we find even *Orthodontium lineare* Mitten as a synonym of *Orthodontium pallens* (Hook. & Wils.) Broth, sensu BROTHERUS: Nepean River, Blue Mountains, leg. WATTS, Oct. 1899, det. BROTH. (herb. K, NSW, H) and coll. Beaconsfield, Tasm., WEYMOUTH 1133, 1892 (herb. BM, H).

The confusion becomes still greater owing to the fact that these specimens are part of *O. sulcatum*, thus something else than the type of *O. pallens*, from Swan river, coll. DRUMMOND, no. 201. We give this example as an illustration of the disorder in the genus, caused by an unsufficient study of types and violations against the rules of nomenclature.

The survey of BROTHERUS (1909) was the first in which the whole genus was considered. Of course BROTHERUS could give only a compilation and in several instances rearrangements, as he dealt with a very comprehensive material and included the moss flora of the whole world. From his compilation and from the use made by others of this work, it appears how confused the taxonomy of exotic mosses is. Orthodontium is apparently not the worst example for, in comparison with others it is a rather small genus. The division given by BROTHERUS (1909) is quite artificial. It is based too much on uncertain characters, such as length of peristome teeth and striation of capsules, a common feature of the whole genus, with the exception of *O. gracile*.

The Orthodontium species of South America, Africa and Australia were not sufficiently compared. *O. brevifolium* Broth. from Africa and *O. loreifolium* Besch. from Réunion, *O. denticulatum*, *O. ulei* C. M., *O. arenarium* C. M. and *O. confine* Hampe from S. America, belong, according to BROTHERUS' treatment, to a different section as *O. fendleri* C. M. and *O. pellucens* (Hook.) Br. eur., from S. America. In fact the last two species are identic with each other and with the last three of the former group, whereas the others are very closely related to *O. pellucens* and to a species of a third section (*O. longisetum* Hampe).

The same confused state of affairs appears from DIXON's paper on Orthodontium in New Zealand (1926), in which he strongly suspected that *O. sulcatum* would have to be reduced to *O. australe* Hook. f. & Wils., but stated furtheron:

"I do not think the problem can be solved satisfactorily except by study in the field."

The naming of Tasmanian Orthodontiums was even more difficult than in New Zealand. RODWAY (1913) gave a key with which no Orthodontium of that region could be named.

O. lineare and *O. lanceolatum*, both of which have capsules sulcate, when ripe, cannot be separated (as RODWAY does) from *O. australe* and *O. sulcatum* on this character.

4. NEW SPECIES AND THE FIRST LUMPING EFFORTS AFTER 1900

Meanwhile further new species were created: *O. haplohymenium* Dixon et Naveau, Central Africa (1927), *O. brevifolium* Broth. from Central Africa (1914), *O. novae-guineae* Dixon from N. Guinea (1942).

All these species are closely related to some taxa around *O. pellucens*, with greater extensions over tropical regions of the world than was hitherto expected (see chapter III). After C. MÜLLER (1905) had already stated that perhaps not more than 23 species could be described in this genus and the total number had increased by 1932 to thirty-one species, of which only 24 were referred to by BROTHERUS (1925), A. LE ROY ANDREWS (1932, 1935) was one of the first who raised some serious doubts against the treatment of the genus by BROTHERUS (1925). He reviewed some forms occurring in North America and investigated their relations with others. He revealed too that studies had been made by MRS. BRITTON in the herbarium of the New York Botanical Garden, of the South American forms, of which four were considered to be identical with *O. pellucens*. It is regrettable that MRS. BRITTON did not publish this important study. Afterwards (1950) LE ROY ANDREWS also joined *O. tenellum*, *O. osculatianum* and *O. gracile* together. The necessity to have a new modern revision of the whole genus on a monographic basis reached a climax when it appeared more and more clearly that W. WATSON's variety *heterocarpa* of *O. gracile*, published from England (1922), which afterwards was found to have spread to Holland and Germany (there described as *O. germanicum* F. and K. Koppe, 1940), is quite different from *O. gracile* (MARGADANT & MEIJER 1950). It seemed hardly possible that this species had been overlooked during decennia of extensive bryological research in these countries, or had recently arisen by mutation, a hypothesis put forward by BURRELL (1940), in a remarkable review of the whole question.

The history of the extension of this form over Europe (MEIJER 1951, see chapter IV) made it more and more obvious that we have to do here with a species introduced into England from another part of the world. This form appeared to fit in the wide variation of the variable African-Australian species *O. lineare* Schwaegr. Another very puzzling Orthodontium was found by GAUME in France and described by ALLORGE and THÉRIOT (1931) as *O. gaumei*. At this point a revision of the whole genus became a necessity, for it soon appeared that all taxonomical problems in Orthodontium are closely linked together and only can be solved by a thorough study of the whole complex genus. The search was now for a better subdivision of the genus, a lumping of the many superfluous species and a more accurate picture of the distribution of the species over the world. In the following chapters such a study has been tried.

CHAPTER III

REVISION OF THE GENUS

1. DESCRIPTION OF THE GENUS

Small acrocarpous mosses, 1—2 cm in height, growing in dense tufts (tufts ± 3 cm), stems densely dichotomous, branching sympodial fastigiate, branches fragile, with many red brown and pale branched rhizoids, with oblique transverse walls, at the base of the stem and from the leaf bases. Stem in cross section with small central cylinder. Chlorophyllous part of protonema sometimes with gemmae (POTIER DE LA VARDE 1950, MEIJER 1951). Gemmae also on rhizoids (Plate II).

Leaves octostichous, erect-patent or recurved, crowded at stem apex, linear-lanceolate, plane or carinate, sometimes twisted, with part of margin reflexed. Length varying considerably on one plant.

Leaf cells hexagonal-linear, oblong, variable in length, but shorter and broader at the brown coloured base, in middle of leaf 10—12 times as long as broad; walls smooth. Leaf margin plane, entire or irregularly dentate near the apex, which is occasionally composed of two cell layers. Costa in most cases ending below the leaf apex, in most cases less than $^1/_4$ of breadth of leaf. Distribution of sexes variable, autoecious, paroecious or rarely heteroecious. Inner perichaetial leaves in male buds reduced, shorter, more concave, sharp pointed, the nerve rudimentary to wanting, paraphyses longer than the antheridia, numerous, with translucent cells, pale yellow, 1—6 antheridia in each bud. Outer perichaetial leaves longer pointed and with distinct nerve. Perichaetial leaves in female flowers somewhat reduced in size, the outer when the capsules are ripe similar to the ordinary leaves. In paroecious flowers antheridia in the axils of leaves under the archegonia. Sporogonia with red brown vaginula at base, seta 1—25 mm, occasionally somewhat bent near apex, tapering into the neck of the sporogonium. Calyptra shining, cucullate.

Lid conical-rostellate, oblique or straight, annulus not differentiated. Capsule oblong-pyriform, sometimes slightly asymmetric, sometimes striate when ripe, in most instances with some rows of thick-walled cells near the mouth. Neck of sporogonium with planeroporous stomata, cells broadly hexagonal, shorter towards the mouth.

Anatomy of sporogonia as on Plate II 1.

Peristome double, inserted below the mouth of the capsule, basal membrane of inner peristome very short or distinct. In most instances outer peristome more robust than inner, but the 16 processes of the inner peristome may be longer than the 16 alternating teeth of the outer peristome. Teeth of outer peristome with median line at the dorsal surface only, ventral surface with transverse joints, not forming distinct lamellae.

Cuticule of peristome smooth or papillose, rarely inner peristome reduced to the basal membrane. Peristome teeth in general erect when moist and incurved when dry.

Differing from *Pohlia* (*Webera*) and *Bryum* especially in the lanceolate or setaceous leaves, the long cells, the structure and mode of opening of the peristome, the peristome always lacking cilia, even rudimentary and without very distinct lamellae at the inner face of the outer peristome.

2. VARIATION OF CHARACTERS

a. The leaves

Having some knowledge of plants of different species, together with their sporogonia, it is very difficult to name a specimen of Orthodontium studying the vegetative parts only. In this respect the genus resembles genera such as *Bryum* and *Pohlia*. By a careful study the section to which a specimen belongs can generally be settled if the student is acquainted with the subtle differences in leaf breadth, form of apex, occasionally dentation, width of the cells and dimensions of the leaves. For the last character it is very difficult to give one standard dimension, because on one single plant the leaves can vary considerably. It is better to compare whole plants than single leaves. Further we have to take into account that the dimension of the leaves can vary according to moisture and light conditions of the habitat.

The glossy appearance of *O. pellucens* and the related *O. infractum* seems to be a rather constant character. It occurs only occasionally in some aberrant forms of *O. lineare*. For the dimensions of the cells no constant figures can be given; they are on the average broader in *O. pellucens* than in *O. lineare* and still narrower in *O. inflatum*. It appears that to a certain extent this character fluctuates, according to different habitats, but the notes about this on the herbarium-labels are few and experimental data are almost totally lacking.

b. Anatomy of the nerves (Plate II)

The nerves show in Orthodontium two different types in cross section. One type is represented by the nerve of *O. gracile*, which lacks definite stereid cells. It is composed of 2—4 layers of cells, of which some may possess a somewhat smaller lumen (fig. 2d). In all the other species we find a definite group of stereid cells in the nerve. At the ventral side of this group two guidecells are found and in some instances a few additional ventral cells and always one row of dorsal cells.

We find in the different forms of *O. lineare* and *O. sulcatum* at the ventral side of the stereid cells one or two cell-layers. This varies accordingly to the extent of development of the leaves. In *O. pellucens* and related forms we only saw one ventral layer.

c. Distribution of the sexes (Plate I)

This can vary in such a way that in some species like *O. lineare* and *O. australe*, which are as a rule autoecious, some antheridia are occasionally found between or below the archegonia. In other cases some archegonia occur in buds with antheridia.

That is the reason that we find in literature different statements about the distribution of the sexes and a great uncertainty about its taxonomic value within the genus.

In our analysis we found always that *O. gracile* is paroecious (antheridia below the archegonia, fig. 4). But this character cannot be used for the discrimination between both sections of Orthodontium (Stableria, including *O. gracile* and Orthodontium, including the other species). In the section Orthodontium, which is generally autoecious and heteroecious, there exists one form which is paroecious (Ruahinerange N. Zealand, herbarium Sainsbury).

In the isotype-collection of *O. haplohymenium* Dixon et Naveau, I found buds with one archegonium and five antheridia. Dixon (1942) reported about his *O. novae-guineae*, that it should be polyoecious, but we could not confirm this on the type material. It seemed to be distinctly autoecious.

O. lineare, *O. sulcatum* and *O. australe* offer examples of heteroecious inflorescenses, e.g. inflorescences where next to male buds, mixed buds occur. We noted this for example in the type collection of *O. sulcatum*, where we found several buds with antheridia on one plant and one where an antheridium was found between archegonia.

We also observed in the type collection of *O. australe* male buds with one archegonium.

We made the following analysis of *Orthodontium lineare* from Germany:

1. Collection Klövenstein leg. Ehrendorff, 1948, herb. Koppe.: On one plant 1 bud with archegonia and 1 antheridium, 1 bud with antheridia, 1 sporogonium with archegonia at its base, together with 1 antheridium. In this connection we could accept that the antheridia near the archegonia were old individuals, arisen in a former growing season, but we found also young antheridia around one non-fertilized archegonium.

2. In another collection (Königsmoor, bei Schmilau) we found one bud with archegonia and two antheridia in the leaf axil below them. We noted in several instances in *O. lineare* that occasionally buds with antheridia are standing quite near the archegonia. Such buds can be strongly reduced. The branch on which they stand may be very short and the number of perichaetial leaves reduced. If this tendency should be strongly developed we should get a paroecious inflorescence. In such a way we discover that in the genus Orthodontium we have to do with the following series of types of inflorescence: autoecious → heteroecious → paroecious. Heteroecious inflorescences were also observed on *O. lineare* by Walsh (1951).

It should be very interesting to investigate the genetic structure and the physiology of growth, which causes this different way of distribution of male and female organs on the plants.

d. Relative length of peristome teeth

In the peristome the relative length of the inner peristome as compared with the outer is a rather variable character.

In *O. australe* and some forms of *O. lineare* the inner peristome

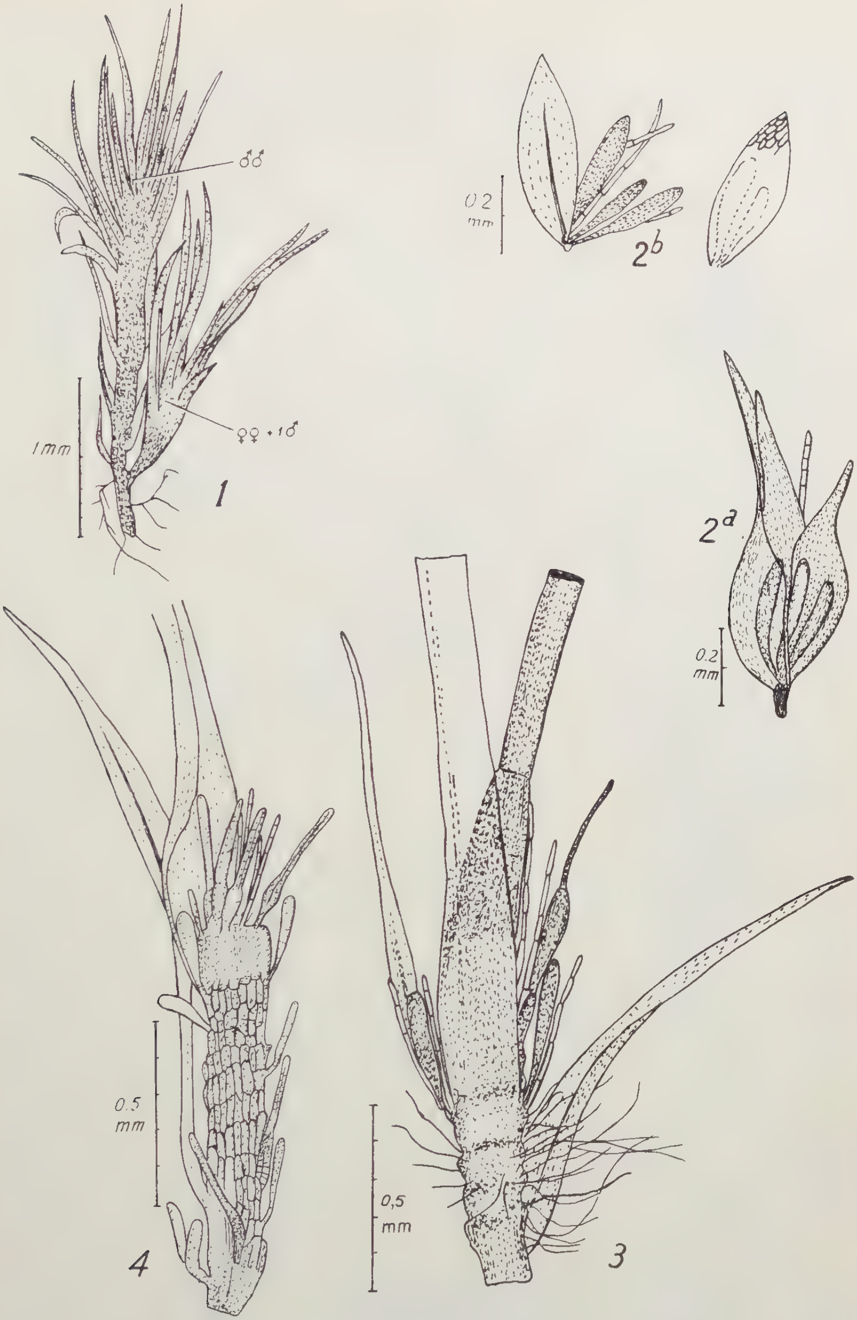

PLATE I

Fig. 1. Plant of *O. australe*, type collection showing buds with antheridia and archegonia.

„ 2. Branches with antheridia of *O. australe*, ssp. *robustiusculum*,
a. leg. Weymouth, Mt. Wellington, Tasm. 3/1893 (NY).
b. leg. Taylor, Tasm. (herb. S).

„ 3. *O. ruahinense*. Type material (Sainsbury no. 9197). Paroecious inflorescence.

„ 4. *O. gracile*. Tunbridgewells, S. England. leg. Wallace & Meijer, 1951. Paroecious inflorescence.

teeth are constantly considerably longer than the outer, but in other forms of *O. lineare* we found in one and the same capsule longer and shorter inner teeth.

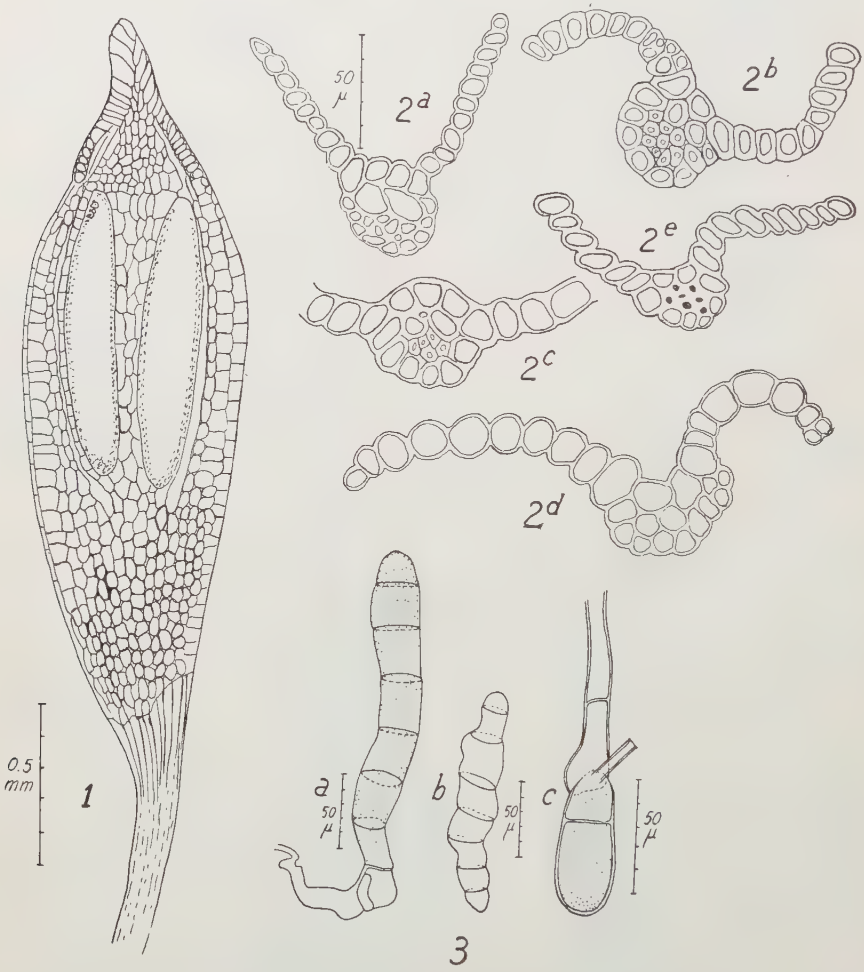

PLATE II

Fig. 1. Longitudinal section of sporogonium of *O. lineare*. Coll. from Doorn, Holland 4—1951.

„ 2. Leaf-sections of
- *a.* *O. ruahinense* (no. 9196, herb. Sainsb.).
- *b.* *O. australe* Falkland Isl. Coll. Halle no. 575 (PC).
- *c.* *O. lineare* leg. Pillans, S. Africa.
- *d.* *O. gracile* Vina del Mar. Musci Sel. no. 245.
- *e.* *O. infractum.*

„ 3. Gemmae:
- *a.* *O. lineare* ssp *sulcatum* (*O. zetterstedtii*, Mt. Williams, Austr.).
- *b.* *O. novae-guineae.*
- *c.* *O. australe* ssp *robustiusculum.*

All observations of the variation of this character show that the discussions on the supposed high taxonomic value of this character were somewhat premature.

The use BROTHERUS (1909, 1925) made of this character for the division of the genus is not justified by the facts. For more details see the discussion of the species.

e. Dimension and shape of the capsules

There are several indications that these characters are not of a great taxonomical value. In the first place in one and the same tuft capsules of very different size can be found.

The smaller capsules also have shorter setae. Comparison of forms of *O. australe* and *O. sulcatum* also indicate however that to a certain extent variations of the length of the setae have a genetical basis, because the relations between length of setae and of capsules are different in these species.

In the second place culture experiments show that the ripening of the sporogonia may start approximately at the same time, both in large older and in younger sporogonia, simultaneously with the reduction division of the spore mother cells. From that time all capsules cease to grow in length and breadth.

Now one of the consequences of this is that ripe capsules comprise large as well as small individuals; another is that microclimate and general climate, influencing the interval between first development of sporogonia and date of the reduction division may modify the dimensions of the sporogonia of a whole population. But these phenomena need further investigation by experiment and by observations in the field. It is regrettable that ecological notes are so scarce in herbaria. Several indications of phenotypical variation are to be found in the discussion of the different forms of *O. lineare* in Europe and in Australia.[1]

f. Juvenile states

Great confusion has been caused in herbaria by the fact that juvenile states of capsules, which resemble the ripe state of other species, are not always recognized as such. The best examples of this are BROTHERUS determinations of *O. pallens* (herb. H). None of this *O. pallens* comprise any specimens of this species. It is an assemblage of young plants of *O. inflatum*, in which the capsules are immature and not yet inflated, together with small forms of *O. lineare*, so called *O. lanceolatum* Mitten.

g. Over-mature capsules

Another extreme is that the capsules may be too old and it has sometimes been wrongly supposed that they have a rudimentary inner peristome where in fact it has been broken away (see DIXON's descriptions of *O. haplohymenium* and *O. novae-guineae*).

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[1] For Australian forms of *O. lineare (O. lineare* ssp *sulcatum)* the name *O. sulcatum* is often used in this paper, as a shortof.

h. Papillosity of peristome

In many instances authors have overlooked the fact that young sporogonia often lack the papillosity, which may be characteristic for the species in question. The same can be true of the small sporogonia ripened in an 'immature' state. Smallness of sporogonia and a smooth peristome can thus be correlated.

If all these phenotypical variations had been born in mind, the greater part of the superfluous species would never have been described, let alone those created only on geographical grounds.

3. HABITAT

The habitats of the different species of the genus are to such an extent similar that it is not necessary to enumerate them under each species.

O. inflatum, *O. pallens*, *O. loreifolium*, *O. denticulatum*, *O. longisetum*, *O. lineare* ssp *piriformis*, *O. australe* ssp *robustiusculum* and *O. novae-guineae* have only been found on old decaying trunks.

All the other taxa occur also on this substrate, but moreover they are gathered on sandy soil, in crevices of rocks, peaty soil and some forms of *O. lineare* ssp *sulcatum* even on burnt logs.

O. pellucens is chiefly found on wood, but occasionally on soil (Tennessee, "*O. arenarium*" in S. America).

O. australe ssp *australe* seems to grow in Fuegia on numerous places in bogs and *Nothofagus* woods.

4. SUBDIVISION OF THE GENUS

The interrelations among the species of Orthodontium can best be expressed by recognizing a number of subdivisions.

O. gracile, including species of the genus Stableria Lindberg, stands apart from every other species in its rather smooth capsule, its paroecious inflorescence, very short basal membrane, and the lack of stereid cells in the costa of the leaves.

A common feature of the *pellucens*-group is that all its species possess glossy leaves. They show a wide variation in peristome structure, forming a series from a simply constructed peristome, with translucent basal membrane and very narrow processes, to a highly papillose robust peristome, with somewhat divided processes. Occasional toothing of the leaves (very pronounced in *O. denticulatum*) and a long beaked lid are other common features of this group. All the species related to *O. lineare* usually possess a more conical lid, and less glossy leaves.

A. In accordance with these considerations the following subdivision of the genus is suggested.

I. Sectio **Stableria** (Lindb., 1878 as genus) Meijer.
Paroecia, foliis setaceis, theca ovato-cuneata, laevissima *(O. gracile)*.

II. Sectio **Orthodontium.**
Autoecia vel heteroecia vel paroecia; folia setacea vel ovato-lanceolata; theca ovato-oblonga, sicca plicata.

a. Subsectio *Pellucens.*
Folia nitida, apice parce denticulato vel integerrimo; operculum rostratum (*O. pellucens* s. l., *O. infractum*, *O. inflatum*).

b. Subsectio *Linearis.*
Folia opaca, integerrima. Operculum brevirostrum vel conicum (*O. pallens*, *O. lineare* s.l., *O. australe* s.l., *O. ruahinense*).

5. Species descriptions and key to the species

ORTHODONTIUM

Orthodontium Schwaegr. Species Muscorum Suppl. II, Sect. 2, 123, 1827, Hook. Ic. Pl. rar. I, Tab. 34, 1837. Bryi sp. Wils. Engl. Bot. Suppl. 3, t. 2835, t. 1839.

Apalodium Mitten, Musc. austr. amer. p. 238. Journ. Linn. Soc., 1869 (= Orthodontium section Orthodontium).

Stableria Lindb. Utkast nat. grup.., p. 20, 1878 (= Orthodontium section Stableria (Lindb.) Meijer.

Key to the species

1*a.* Plants paroecious, leaves rather narrow setaceous; costa without stereids; capsule smooth when ripe. 1. **O. gracile**

b. Plants paroecious, autoecious or heteroecious; capsule in most cases sulcate when ripe, costa with stereids 2

2*a.* Capsule ovate-pyriform, inner peristome on a translucent very thin basal membrane, with very thin and narrow processes 3

b. Capsule not pyriform, or with a firm inner peristome . . 4

3*a.* Leaves setaceous, with narrow cells (± 7,5 μ), sporogonia distinctly swollen when ripe . . . . . . 6. **O. inflatum**

b. Leaves broader, lanceolate or ovate-lanceolate, capsules pyriform-ovate, usually not swollen; leaves occasionally toothed near apex . . . . 7. **O. infractum**

4*a.* Leaves linear-lanceolate (± 5 mm broad), rather suddenly tapering at apex or more gradually, with a metallic glance, occasionally or regular toothed near apex. Cells at middle of leaf 12—18 μ broad. Lid rather long beaked (0,35—0,95, at average 0,70 mm). 8. **O. pellucens** s.l. (compare 8*a*—8*e*)

b. Leaves usually narrower, more gradually and longer tapering at apex, margin only rarely with some irregular teeth near apex, usually not glossy, cells narrower (± 10—12 μ) at midst of the leaf. Lid of sporogonium shorter (max. 0,40 mm) 5

5*a.* Inner peristome rudimentary, with high basal membrane, adherent to the outer peristome . . . . . 5. **O. pallens**

b. Inner peristome well developed in ripe capsules, in older capsules sometimes broken away 6

6*a.* Plants only paroecious. Several rather short setae on one stem, occasionally the lower reached by the setaceous upper leaves . . . . 2. **O. ruahinense** *b.* Plants generally autoecious, occasionally heteroecious, usually with one sporogonium on one plant 7

7*a.* Leaves erect-linear, with strong nerve, in upper part of leaf 1/4—1/3 of leaf breadth. Capsule oblong-lanceolate, seldom somewhat ovate-pyriform. 4*a.* **O. australe** ssp **australe**

b. Leaves erect-spreading, broader; capsule more generally lanceolate-ovate 8

8*a.* Robust plants, with long setae (11—25, average 20 mm) and large capsules (length 2,5—3,0 mm). Inner peristome up to ± 185 μ in length. 4*b.* **O. australe** ssp **robustiusculum**

b. Smaller plants, with shorter setae (5,5—13, average 8 mm) and smaller capsules. Inner peristome up to 280 μ in length. 3. **O. lineare** (compare 3*a*, 3*b* and 3*c*)

1. **Orthodontium gracile** Schwaegr. ex Br. et Sch. Bryol. eur. fasc. 3—4, 1844. (in litt. ad Wilson).

Bryum (*Pohlia*) *gracile* Wilson, Gardner. Muscol. Brit. T. 34, App. (1839); Suppl. to the English Botany of the late Sir J. E. Smith and Mr. Sowerby 3, t. 2835 (1839); holotype in herb. WILSON (BM).

Orthodontium aethiopicum C. M. Bot. Zeit. 13, Oct. 1855.

Stableria aethiopica (C. M.) Broth. Engler & Prantl. Die Natürliche Pflanzenfam., 10, (1st. ed.), 1909; lectotype in herb. S.[1]

Orthodontium laxirete Dusen. nom. nud.; herb. S.

Orthodontium osculatianum De Not. Mem. della Reale Accademia delle Scienze di Torino. Series 2, 18; 444. t. 4, 1857, holotype in herb. Rome.

Orthodontium tenellum Mitt. Musci austro-americani. Journ. of the Linn. Soc. Bot. Vol. 12, 1869; holotype in herb. NY.

Stableria tenella (Mitt.) Broth. Engl. & Prantl., 10 (1st ed.), 1909.

Orthodontium peruvianum Hampe nom. nud.; in herb. BM.

Orthodontium setaceum W. P. Sch. nom. nud., in Mandon Pl. Boliv. n. 1658; type in herb. K.

Orthodontium lineare Schwaegr. p. p. Wilson 1839. Suppl. Eng. Bot.

Description:

Paroecious plants, in dense tufts, variable in height ($^1/_2$—7,5 mm), with long pointed, narrow setaceous leaves (1—7 mm), often twisted, or patent. Cells in middle of leaf ± 8—12 μ broad. Sporogonia sometimes several on 1 plant, seta 2,5—10 mm large. Capsule varying from ovate to narrow lanceolate or wedge shaped, with contracted or wide mouth, extremely variable in dimensions (from 1,2 × 0,40—2,0 × 0,80 mm, 1,8 × 0,50 at average). Capsule walls light brownish-yellow. Walls when dry slightly irregular sulcate or smooth. Margin of capsule bordered with 3—4 rows of cells with thin walls and one row of longer cells, forming the transition to the oblong cells beneath them. Colour of the bordercells only slightly darker than the other. Lid conical or shortly rostrate.

Peristome smooth. Outer teeth 6—9, usually with 7 joints,

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[1] For abbreviations of herbarium names used see Acknowledgements (p. 77), WM refers to the herbarium of the author.

108—260 μ long, $\pm$ 40 μ broad at base, margin gradually tapering towards apex. Processi of inner peristome equal, somewhat shorter, or longer in length, much narrower; breadth about 5 μ, for most of their length, $\pm$ 25 μ at broadened base. Median line only visible in the lower part. Spores 10—18 μ in diameter. (Plate I 4, II 2d, III, IV.)

Discussion:

A variable plant. Variation is however found only in the dimension of the different parts of the plant and in the shape of capsules. The smallest plants (seta 2,5 mm), with the smallest sporogonia are the specimens of *O. laxirete* nom. nud. from South Chile.

Generally more robust are the *O. tenella* forms from W. and Central Africa and from South America. The capsules of this form are usually rather oblong pyriform. Ripened juvenile states however bear much narrower and smaller capsules (Plate III). These are quite comparable with *O. gracile* from England. Some of the English specimens however are more like typical *tenella*-forms (Plate III).

The French specimens and "*O. aethiopicum*" also bear more normal capsules. The same is true of *O. osculatianum*, *O. peruvianum* and *O. setaceum.* From several observations it appears that *O. gracile* in England is living near the limit possible for its existence. After severe winters the capsules are damaged, white coloured (Litt. BURRELL, 1940 & herb. WILSON). The small South Chilean form is perhaps also formed under the influence of a colder climate. I have tried honestly to find real differences between the described species of the section Stableria (formerly as a genus, LINDB., 1878), but I cannot find any real species limitations in this group.

We should not exclude the possibility that within the series of variation in *O. gracile*, from the equator till northwards and southwards, geographical clines in the sense of HUXLEY (1940) may exist. Without culture experiments it is of course impossible to state to what extent these differences are genetical.

Examined specimens:

England: Cheshire, Helsby, leg. W. Wilson, 25(—27) March 1833 (BM type; PC, S), March 9, 1836 (W), 1842, 1846 (S); G. E. Hunt, 1868 (S), 1870 (S), W. P. Schimper, 1865 (S); W. Curnow (S, L); Dr Wood (S), Alderley leg. Wood (S); Frodsham, leg. Hund (S).

Alderley Edge, Sandstone rocks, leg. Hurst, 1863, un. itin crypt. W. Ph. Schimper, 1865 (L, PC), W. W., 1896 (K). Peckforton Hill, leg. Armitage, 1916 (K). Yorkshire, V.C. 64, Strid Bolton Abbey., leg. W. H. Burrell, 1923, (Br.), 1927, no. 477 (W), 1830, herb. Baker (U.S.), Bolton Woods, Ingham (PC); Skripton, leg. Lapworth, 1919 (K); Sussex, Rocks at Wakehurst, leg. Hennings, 1854 (U.S.). E. Sussex, V.C. 14, Rocks in Chiddingly Wood, leg. A. Comyn, 1951 (WM. ex herb. F. Rose); Lower Pennrocks, leg. Wallace & Meijer (WM), N.W. of Buxted, Sandstone rocks, leg. F. Rose 1951 (WM). Kent, Eridge rocks, 1844 (Br.), leg. Jameson 1888, 1894 (K), Nicholson, 1913 (U.S.), 1919 (K), Wallace 1946 (WM.), Wallace & Meijer, 1951 (WM.).

Wales: Nant y Ffrith, Flintshire, V.C. 51; leg. Jones and Rhodes, Bauer Musci europ. 1775 (S, Br.). Ffrith, Flintsh. leg. Watson, 1913 (S).

Scotland: Rosslyn Glen, Edinburgh, leg. W. Evans, 1900 (K).

France: Bretagne, leg. Husnot. Musc. gall. no. 665. Finistère (Bannalec, Scaer).

Central Africa, Congo: E. de Nirraganga, 2900 m, Lebrun 8737 (Br.), Shaheru, Lebrun 9356 (Br.), versant N. d. Karisimbi 3900 m, alpage à bruyères et Senecios arboresc, epiphyte s. Philippia, Louis 5350 (Br.) Karisimbi Louis 1347B; entre Kabara et Rakumi versant N. du Karasimbi, Lebrun 7393, 1937 (WM ex Br.).

Cameroon: Montane forest, above Ukile, Cameroon Mountain, Br. Cameroons, ca. 8500 ft, leg. P. W. Richards no. 4298, 1948 (WM).

Abyssinia: leg. W. Schimper, Cosso Berri: 11200 ft (L; S lectotype of of *O. aethiopicum* C.M.; MEL).

America, California: Buxham Ranch. Sonoma, L. J. Koch, 1939 (herb. Bartram); Mendocina, leg. Howe 1896. (herb. Le Roy Andrews).

Guatemala: Chiquiral, Quetzattenango, 8200 ft, leg. Sharp, 2135, 1945 (herb. Bartram, det. as *O. pellucens*), East of Totouicapan, 10.500 ft, 12618, 1945, coll. Sharp (herb. Bartram det. as *O. pellucens*).

Colombia: ad Mt. Napi, leg. Osculatis, *O. osculatianum* de Not., (isotype in herb. L.); Andes Quintensis, [herb. Hooker (K), isotype of *O. tenellum*, Mitten].

Peru: Gay no. 2044, 1839—1840 (PC; BM, type of *O. peruvianum*).

Bolivia: Vicinus Sorata, Prov. Larecaja, 3200 m, 1858. Manson, Plantae Andium Boliviensae no. 1658; as *O. setaceum* W.P. Sch., nom. nud., (herb. PC, type in herb. K.); Sorata, 2500 m, leg. Williams, no. 1706, 1902 (K).

Chile: Chile australis, insula Quiriquina, leg. P. Dusen, 1896, type of *O. laxirete* Dusen, nom. nud. (in herb. S, NY, PC, FH). Vina del Mar, Salto, leg. Bertho; 1934; det. Thériot as *O. tenellum* Mitten, Musc. Sel. et Crit. ed. Fr. Verdoorn, V (1938). (L, herb. Amsterdam).

2. **Orthodontium ruahinense** Meijer, nov. spec.

Latin diagnosis:

Paroecum. Plantae humiles, cum tomento fusco in basi; folia gradatim setacea, siccata crispata; nervus modice distinctus, cum cellulis stereidis, evanescens ante folii apicem; aliquot sporogonia superposita in uno caule, aliquando sporogonio infimo paulum folio oculto. Capsulae atque setae longitudine diversae; capsulae forma ovata-cylindriaca; capsula laevis vel paulum sulcata, cum collenchymateis cellulis ad marginem. Peristomium in explorato specimine non distincte papillosum. Operculum et sporae nondum inventa.

Description:

Paroecious. Small plants, at base with brownish tomentum. Leaves gradually setaceous, 2—7 mm, somewhat curled when dry. Costa rather distinct, with stereid cells, ending before the leaf-apex.

EXPLANATION OF PLATE III

Capsules of *O. gracile* from different parts of the world.

a. Leg. P. W. Richards, Br. Cameroon. 1948, no. 4298. Both capsules of this collection!
b. Leg. Hunt, Cheshire, England, 1868 (S).
c. Leg. W. Schimper, Abyssinia C.M.
Isotype of *O. aethiopicum* (S).
d. *O. peruvianum* Hampe nom. nud. Peru, (isotype PC).
c. Coll. Sharp no. 2618, Guatemala (herb. Bartram).
f. Coll. Louis, no. 5350. Congo Belg. (Br).
g. and *h:* coll. Lebrun, no. 9356. Congo Belg. (Br).
i. Pennrocks, Tunbridgewells, S. England. Leg. Wallace & Meijer, 12-4-51.
j. Eridgerocks, Kent. S. England, 1844 (Br).
k. Bolivia type of *O. setaceum* W. P. Sch. nom. nud., type in herb. K.
l. and *m.* Guatemala. Coll. Sharp, no. 2135 (herb. Bartram).

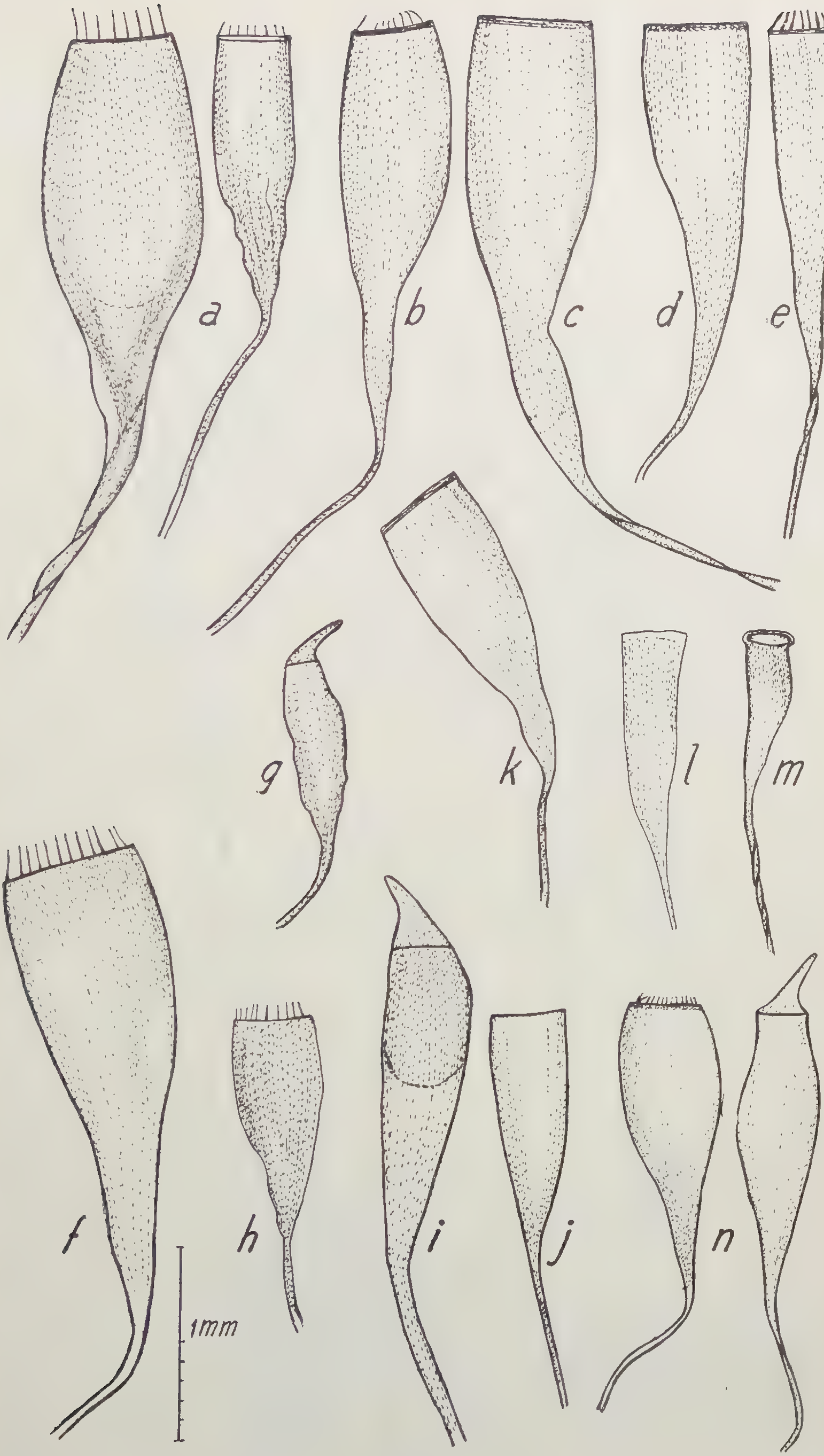

PLATE III

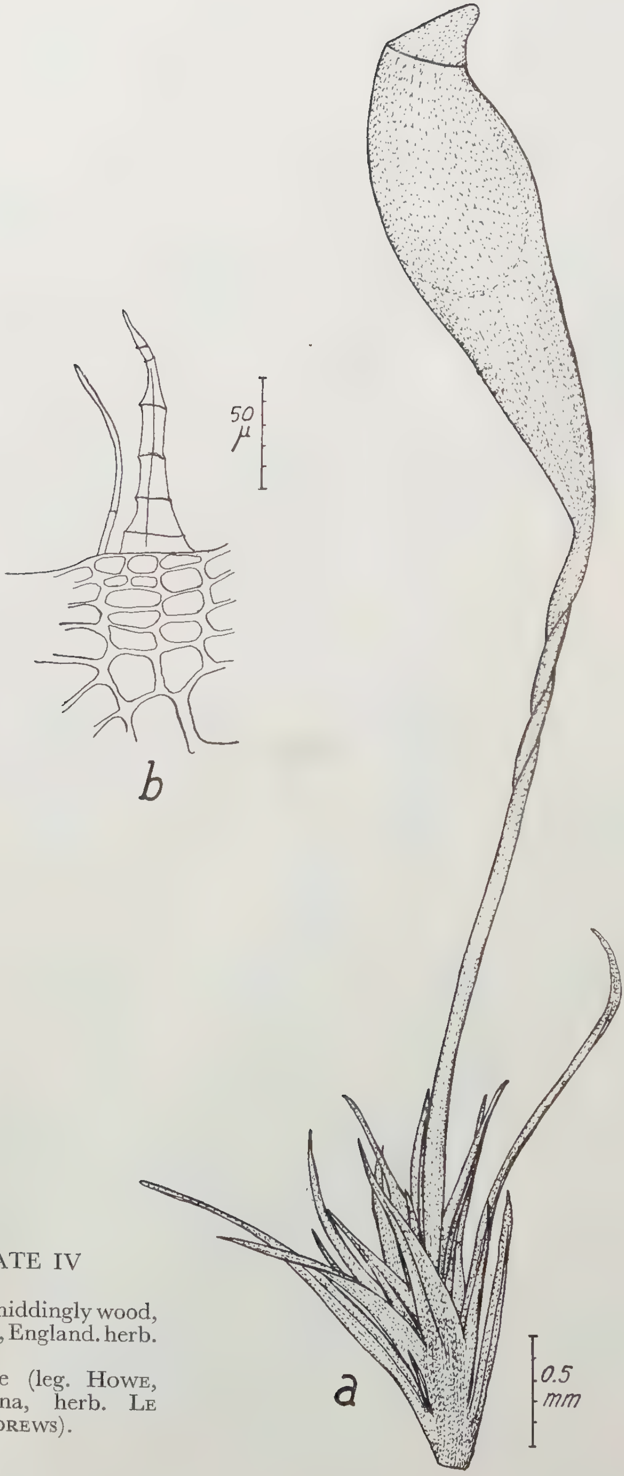

PLATE IV

O. gracile:

a. Habit. Chiddingly wood, E. Sussex, England. herb. ROSE.

b. Peristome (leg. HOWE, Mendocina, herb. LE ROY ANDREWS).

Sporogonia several above each other on one stem, occasionally the lowest somewhat hidden by the leaves. Capsules as well as setae of different length. Shape of the capsule ovate-cylindrical. Capsule wall smooth or slightly sulcate; with collenchymatous cells near the margin. Peristome rather simply constructed, not distinctly papillose in the examined specimen. Lid and spores unknown (Plate I 3, II 2a, V).

Discussion:

Closely related to narrow-leaved forms of *O. lineare* ssp *sulcatum*. Different from that in its paroecious inflorescence, the somewhat longer setacious leaves and the rather small peristome.

In habit strongly resembling *O. gracile*, because the leaves are narrow and long, the plants bear several setae, situated on the same stem and the form of the capsules is rather similar.

I first supposed that it should belong to that species, because it has the same habit. A more detailed investigation revealed however, that it possesses the following characters of section Orthodontium: collenchymatous cells near the margin of the capsule mouth and stereid cells in the costa. The peristome resembles that of *O. gracile* in its dimensions and its smoothness, but the processes are broader.

The leaftype is similar to that of narrow-leaved forms of *O. sulcatum*, but even more setaceous. While the difference autoecious (or heteroecious) against paroecious is in general a good distinguishing character between the species of the section Orthodontium and *O. gracile* (section Stableria), its great usefullness in the subdivision of the genus breaks down here.

Of course it should be possible to minimize the importance of the sex relations totally and to consider this form as a variant of *O. lineare* ssp *sulcatum*. But then we should neglect the fact that it differs also in the other respects, indicated above, from that taxon. Nevertheless the distribution of this peculiar form, which has been gathered only twice on approximately the same place in New Zealand, deserves a further study.

Especially its relation to the narrow-leaved forms of *O. sulcatum* should be further investigated. We accept here that it has its own position as an endemic species in New Zealand.

Examined specimens:

Type: N.W. Ruahine Ranges, N. Island, N.Z., leg. A. P. Druce Jan. 1948, herb. G. O. K. Sainsbury no. 9197.

Other collection, same locality, collector and date: herb. G. O. K. Sainsbury no. 9196.

Mr. Sainsbury kindly informed me that these specimens are growing on a very rugged place in the island, not easily accessible.

3. **Orthodontium lineare** Schwaegr, Species Muscorum, Suppl. 2, Sect. 2: 123—125, Plate 138. Holotype in herb. Geneva.

Apalodium lineare (Schwaegr.) Mitten. Voy. H. M. S. Challenger, Bot. IV, p. 198, in adn., 1885, non *Apalodium lineare* (Taylor) Mitten. Trans and Proc. Royal Soc. of Victoria, vol. 19, 1883.

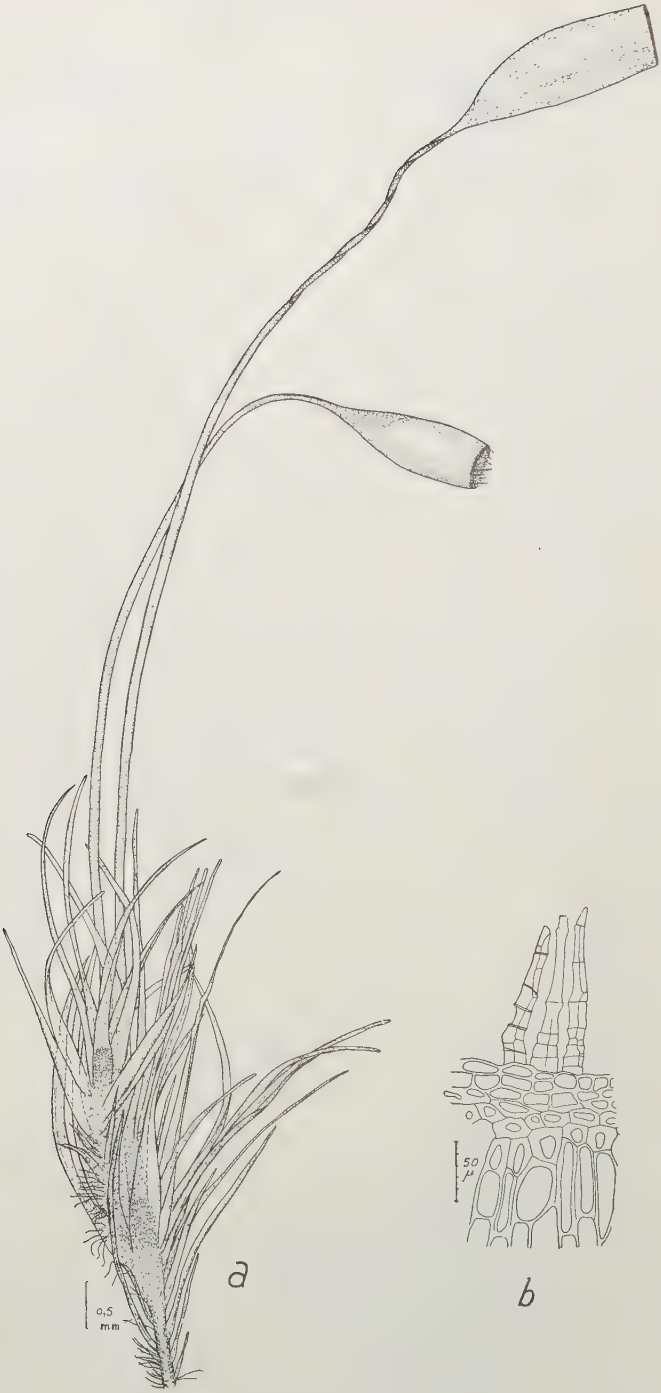

PLATE V

O. ruahinense:
a. Habit of type mat., N. Zealand. (herb. Sainsbury no. 9196).
b. Peristome (New Zealand, leg. Druce, herb. Sainsbury no. 9196).

Orthodontium gracile Schwaegr. ex Br. et Sch. var. *heterocarpum* Watson, Journal of Bot. 60: 139—41, 1922.

Orthodontium germanicum F. et K. Koppe. Fedde Repert., Beiheft CXXI: 40—47, 1940.

a. **Orthodontium lineare** Schwaegr. ssp **lineare.**

Description:

Autoecious plants, with crowded, dull green, gradually tapering, rather narrow, erect and recurved leaves (max. breadth c. 0,4 mm, max. length 2—6 mm). Cells in middle of leaf at the average 12 μ broad, thin walled. Seta 6—13 (av. 8) mm long. Capsule erect or somewhat bent, globose-ovate, rather short neck, before ripeness contracted at the mouth, which is bordered with thin-walled cells, above some red brown collenchymatous rows.

Lid conical or rostellate. Capsules variable in dimension (0,8—2,5 mm) × (0,4—0,9 mm), sulcate or smooth when dry. Peristome varying in length, accordingly to the dimensions of the capsules; outer teeth somewhat papillose, 75—150 μ in length, 25—35 μ broad at base; segments in inner peristome 70—220 μ in length, 10—15 μ broad at base, papillose, especially near the summit, composed of 6—8 joints. Basal membrane of inner peristome some cells high, with distinct median line, finely papillose. The whole peristome pale coloured. Relative length of outer peristome and segments of the inner variable even within one capsule, equal in length, or the inner segments considerably longer. Spores 15—20 μ. (Plate II 2, VI).

Discussion:

Very closely related to *O. lineare* ssp *sulcatum*, but distinguished from that by a narrower variation of gametophyte characters. The leaves have a more uniform character; they are always narrow acuminate.

The peristome type of *O. australe* resembles that of *O. lineare* ssp *lineare*. The differential characters of *O. australe* ssp *australe* are: seta generally longer, capsule usually more oblong, peristome with a stronger tendency to an equal length of inner and outer teeth, leaves with broader nerve.

O. australe ssp *australe* has a more robust peristome (max. length of teeth 280 μ) and the leaves are somewhat longer and broader. *O. lineare* ssp *piriformis* has a more pyriform capsule, smaller and more glossy leaves and a more rostellate lid.

For a further illustration of these differences we give here our measurements of various characters in *O. australe* ssp *australe*, *O. australe* ssp *robustiusculum*, *O. lineare* ssp *lineare* and *O. lineare* ssp *sulcatum*.

From a study of this table it will be evident that *O. australe* ssp *australe* and *O. australe* ssp *robustiusculum* differ from *O. lineare* ssp *sulcatum* and *O. lineare* ssp *lineare*, in the somewhat smaller maxima of leaf-length and in higher maxima of length of seta.

The maximum dimensions of the peristome and the spores in

O. australe are considerably greater than in *O. lineare* and the minima differ even more widely.

Between *O. lineare* ssp *sulcatum* and *O. lineare* ssp *lineare* the differences in these dimensions are very slight. The minimum size of the capsules of *O. sulcatum* may be somewhat smaller than of *O. lineare*.

TABLE I

Comparison of some taxa

Taxon:	australe	robustiusculum	sulcatum	lineare
1. Max. length of leaves in mm	4,5	5	6	6
2. Breadth of cells at middle of leaves in μ	8—11	10—12	9—14	12
3. Length of seta in mm	5—20	11—26	4—13	5—13
4. Dimensions of capsules in mm:				
length	1,9—2,5	2,5—3,2	0,8—2,5	1.1—2,4
breadth	0,5—0,6	0,7—1,0	0,4—0,9	0,45—0,90
5. Length of outer peristome in μ	130—195	110—250	100—170	70—150
Length of processes in μ	180—290	160—280	100—230	70—220
6. Diameter of spores in μ	12—23	15—24	15—20	15—20
7. Length of lid in mm	0,4—0,5	0,7—	0,5	0,5

It ought to be stressed that these figures give only an impression of the range of variation of the characters. The material which is available is too small (c. 160 specimens of the whole subsection *Linearis*), to give any reliable figures of the variation. Only some tendencies can be shown. Moreover the differences between *O. lineare* ssp *sulcatum* and *O. lineare* ssp *lineare* are somewhat greater than appears from the figures given in above table, because *O. sulcatum* shows a greater variation of leaf types and of peristome characters. The outer peristome especially has a tendency to remain smooth, while the inner is usually papillose.

O. lineare ssp *lineare* and *O. lineare* ssp *sulcatum* possess so many characters in common, that they partly cannot always be separated; they are thus typical examples of geographical subspecies. Of these two subspecies the australian ssp *sulcatum* is the richest in characters, as will be shown below.

EXAMINED SPECIMENS:

S. Africa: Cape, leg. Menzies, holotype, herb. Hedwig-Schwaegrichen (Geneva); George, Cape Colony, leg. H. A. Wager, 1906, no. 542 (BM); South of Great Kop, Cape Peninsula, leg. N.S. Pillans, 4271, 14 Jan. 1923 (BM, PRET).

EXPLANATION OF PLATE VI

O. lineare ssp *lineare:*

a. Habit (coll. PILLANS no. 4271, herb. PRET).
b. older sporogonium (coll. WAGER, George, Cape Colony, BM).
c. Young sporogonium (coll. Naardermeer, Holland).
d. Leaf apex. 1. *O. lineare* (coll. BURRELL 1923, England) PC.
e. Base of leaf (same coll.).
f. Peristome (Doorn, Holland, leg. W.M.).

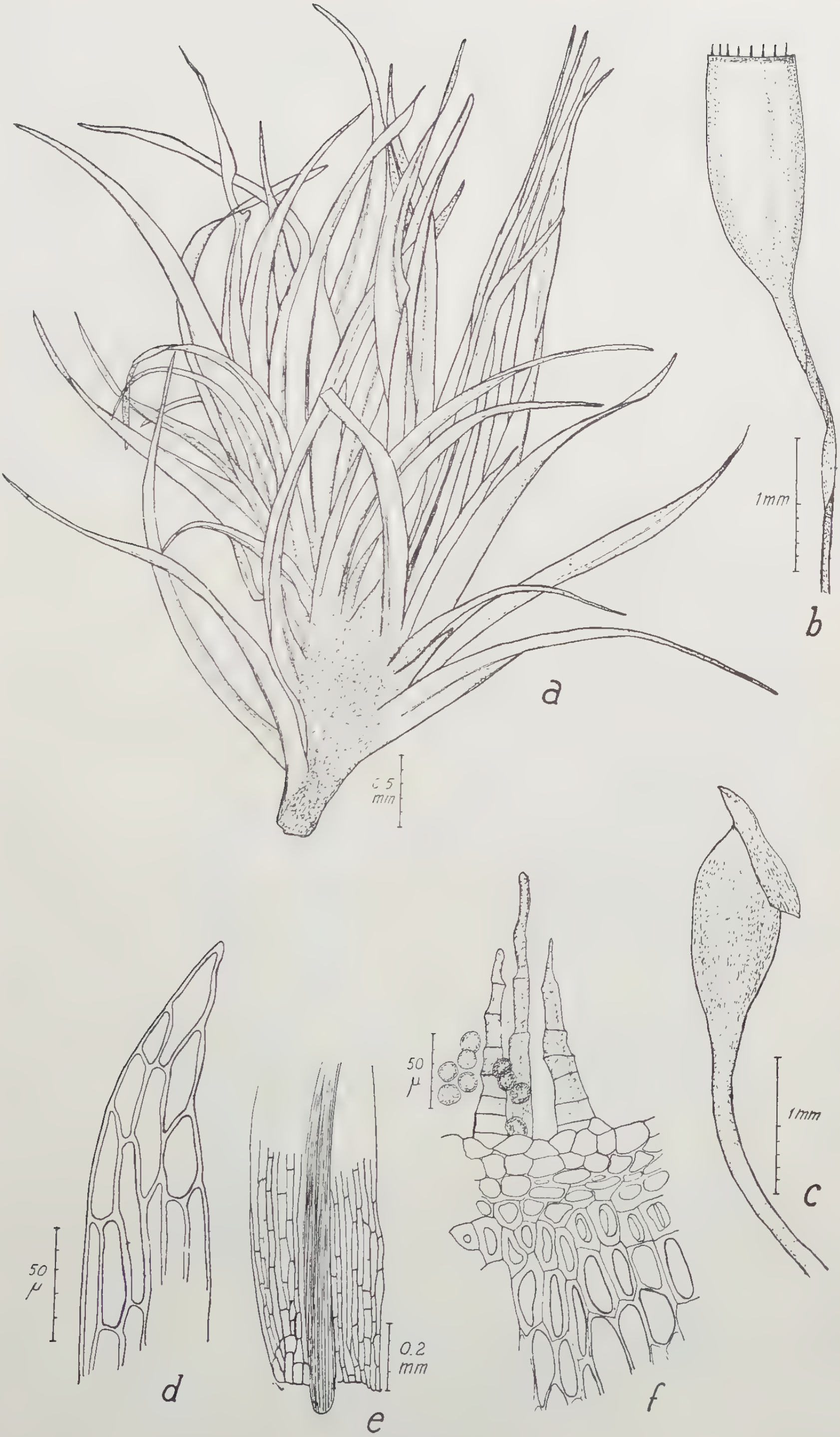

PLATE VI

England: V.C. 11, Wood N.E. of Bagshot, leg. F. Rose. 1951 (WM); V.C. 12, Blackmoor, Golfcourse nr. Borden, 300ft, leg. F. Rose & E. C. Wallace, 1951 (WM); VC 14, (Sussex), Lower Pennrocks, leg. F. Rose, 1951 (WM); The Rocks, Uckfield, E. Sussex, leg. F. Rose, 1951 (WM); V.C. 16, Pettswood, leg. F. Rose, 1949 (WM); V.C. 24, Black Park, Hangley, leg. F. Rose, 1950, (WM); V.C. 58 (Cheshire), Gritstone rocks, Crowden, leg. Broome & W. Watson 1920, type coll. of var. *heterocarpum*; Watson (K) Overton Hills, leg. E. A. Richards, 1911 (BM, earliest collection, as hitherto known); Laddow rocks, leg. W. Watson, 1927 (BM). V.C. 54, Laceby, leg. G. H. Allison, 1934 (K); Yorkshire. Yearsly moor, leg. E. C. Wallace, 1946 (WM); Harrogate, herb. Stevens (K); Midhope moor, leg. Burrell, 1923 (K, PC, BM); V.C. 61, E. Yorkshire, Shipwith common, 50 ft, leg. Burrell, 1935 (herb. Bartram, U.S.); V.C. 62, W. Yorkshire, Brewham, Sandstone rocks, leg. E. C. Wallace 542, 1943 (WM); N. E. Yorkshire Buttercrumbe Moor, leg. F. Rose, 1948 (WM); V.C. 63 Ramsdon rocks, Holmferth, leg. Milson, 1924 (K); V.C. 67, E. Ebington, nr. Hayden Bridge, 1939, leg. E. M. Lobby, (herb. Bartram 374).

Holland: Thijssesbos, Naardermeer leg. W. Vergouw & W. Meijer, 1943, leg. WM, 1949 (WM); Zonneheuvel, Doorn, 1949, 1951. leg. WM (WM). Schovenhorst, Putten 1950. leg. Bryol. Werkgr. (WM); Heelsumse beekdal, Heelsum leg. E. Nannenga-Bremekamp, 1950, 1951 (WM).

Germany: Ex. herb. F. Koppe, in herb. WM: Eberswalde, Brandenburg, Kreis Oberbarmin, leg. K. Koppe, 1939, type of *O. germanicum* F. & K. Koppe; Lauenburg, Königsmoor bei Schmilau Elmendorff, 1950; Klövenstein Jg. 12, 1948, leg. Elmendorff.

b. **Orthodontium lineare** Schwaegr.
nov. subspec. **piriforme** Meijer.

Latin diagnosis:

foliis breviter subulatis, parce nitidis; seta 6—7 mm; theca piriformis; operculo rostellato; peristomium internum papillosum, externum laeve; sporae 15—25 μ.

Description:

Differs from *O. lineare* Schwaegr. subsp. *lineare* in its more glossy leaves, in the typical pyriform sporogonia and the rostellate lid. The peristome is papillose on the endostome only, the dimensions of the spores are rather large (15—25 μ). Type no. 16629, coll. L. J. Brass. Vernay Nyasaland Expedition 1946 — Luchenya plateau. Lower part of trunk of a *Widdringtonia* tree, 2000 m alt., July 3, 1946.

Other collections from the same region and the same expedition, collected by Brass are: no. 16540. Small patch on trunk of a forest tree in deep shade, 1890 m alt., June 30, 1946 and no. 1645: exposed crown of a tall *Widdringtonia* tree, 1890 m. alt. June 30, 1946 (all herb. Bartram). (Plate VII).

Discussion:

This peculiar form has been determinated by Dr Bartram as *O. lineare* Schwaegr. I agree with him, but in my opinion the above named differences from *O. lineare* Schwaegr. from the Cape indicate that it may be named a geographical variation of that species. The glossiness of the leaves give it an appearance of a member of the subsection *Linearis*. It seems however to me to be too closely related to *O. lineare* Schwaegr. to describe it as a new species.

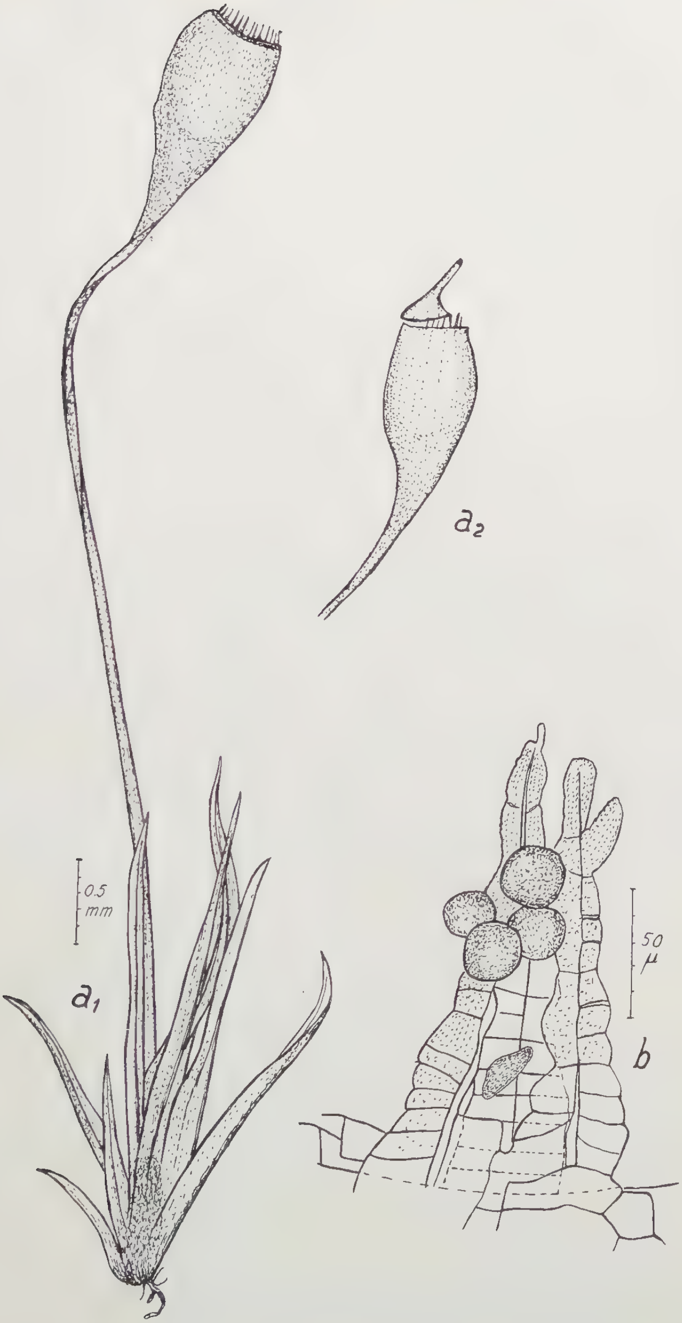

PLATE VII

O. lineare ssp *piriforme:*
a.$_1$ Habit. Nyasaland, coll. Brass. no. 16545 (herb. Bartram).
a.$_3$ Capsule, coll. Brass. no. 16540, (herb. Bartram).
b. Peristome, coll. Brass no. 16629 (herb. Bartram).

c. **Orthodontium lineare** Schwaegr. ssp **sulcatum** (Hook.f. et Wils.) Meijer, comb. nov.

Orthodontium sulcatum Hook. fil et Wils. Hooker Icones Plantarum, Vol. IV, New Series 1848. Tab. 739 B; type in herb. Wils. (BM)

Apalodium sulcatum (Hook. f. et Wils.) Mitten. Austr. Mosses. Trans. & Proc. of Royal Soc. of Vict. 19: 49—96, 1883.

Orthodontium lanceolatum Mitten. Hookers Journ. of Bot. and Kew Garden Mescallany. 8, 1856; type in herb. NY.

Apalodium lanceolatum (Mitten) Mitten; Trans. & Proc. Royal Soc. of Vict. 19: 49—96, 1883.

Orthodontium zetterstedtii C. M. Symb. ad Bryol. Austr. Hedwigia 37: 76—171, 1898; type in herb. MEL.

Based on erroneous determinations are:

Apalodium lineare Auct. non (Taylor) Mitten; Watts & Whitelegge 1905, Census musc. Austr. Proc. Linn. Soc. of N.S. Wales. Suppl.

Orthodontium pallens Auct. non Hook. fil. et Wils; Watts & Whitelegge 1905, lit. cit.

Description:

In habit and dimensions of gametophyte and sporophyte similar to *O. lineare* ssp *lineare.* Autoecious or heteroecious.

In the typical common form the leaves are somewhat shorter pointed than in ssp *lineare*. But forms with narrow pointed leaves or even broader leaves also occur. The last have approximately the leaf type of the subsection *Pellucens.* The apex of those leaves can also be toothed occasionally. Peristome smooth, or only the inner processes papillose, or sometimes both the processes and the teeth of the outer peristome papillose. Processes on distinct basal membrane, texture and dimensions of the peristome as in ssp *lineare.* Lid of sporogonium conical or shortly rostellate. Form, margin and sulcation of the sporogonium similar to *O. l. lineare.* (Plate II 3a; VIII, IX and X.)

Discussion:

Hooker & Wilson (1848) wrote after the original description: "Allied to *O. lineare* Schwaegr., but differing essentially from that and the other species in the furrowed capsule. The leaves also are shorter and not gradually tapering".

We have shown however that the capsules of *O. lineare* and of *O. australe* may be sulcate too when ripe. Hooker & Wilson saw only a drawing of *O. lineare* and specimens of *O. australe* with young smooth capsules. Later bryologists followed in the steps of Hooker & Wilson,

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EXPLANATION OF PLATE VIII

O. lineare ssp *sulcatum:*
a. Narrow leaved form. (Coll. Bell. N. Zealand, Jan. 1887, H).
b., c. and *d.* type of *O. lanceolatum* Mitten (NY).
b. habit.
c. capsule.
d. peristome.

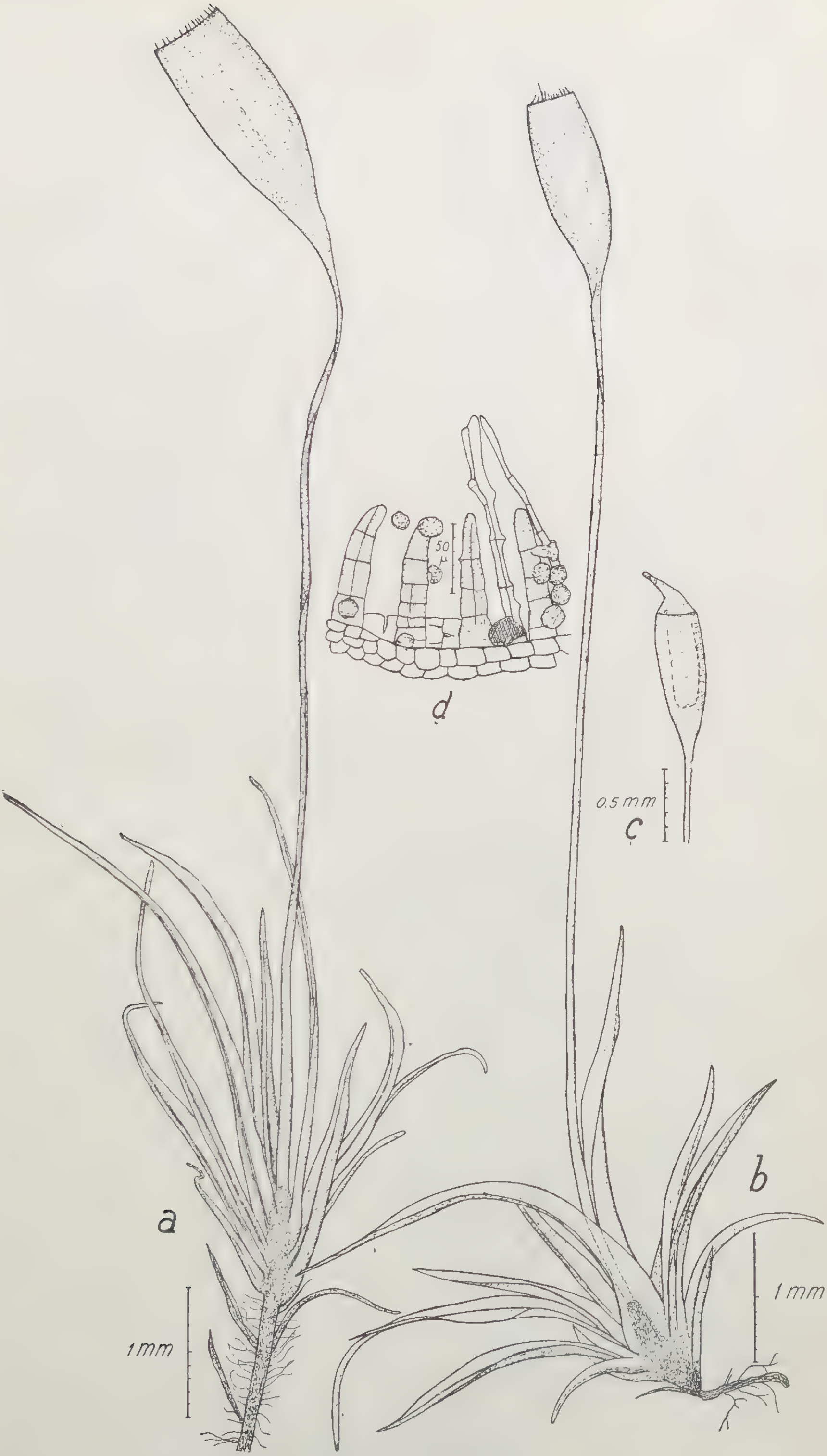

PLATE VIII

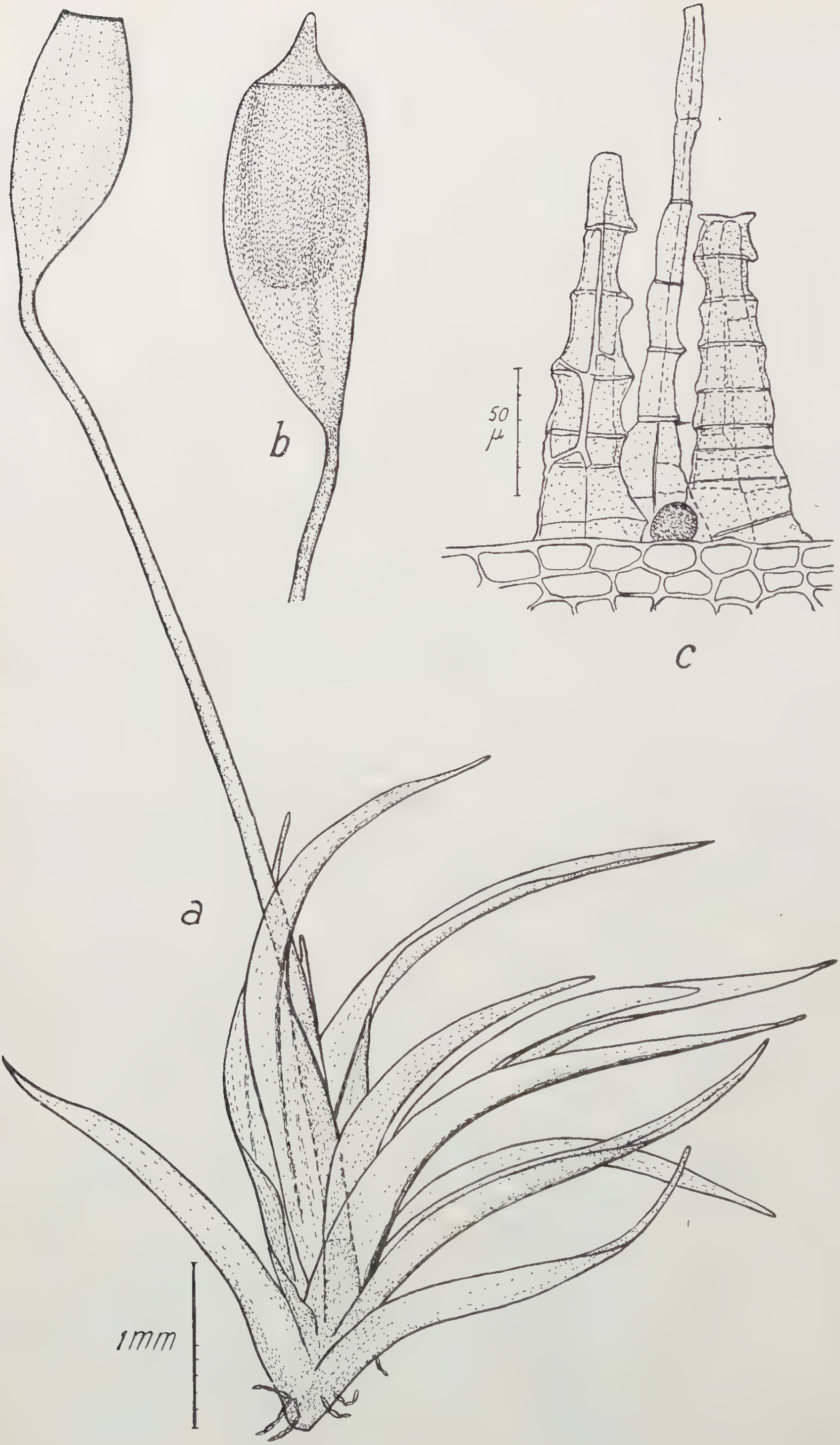

PLATE IX
Explanation on page 38

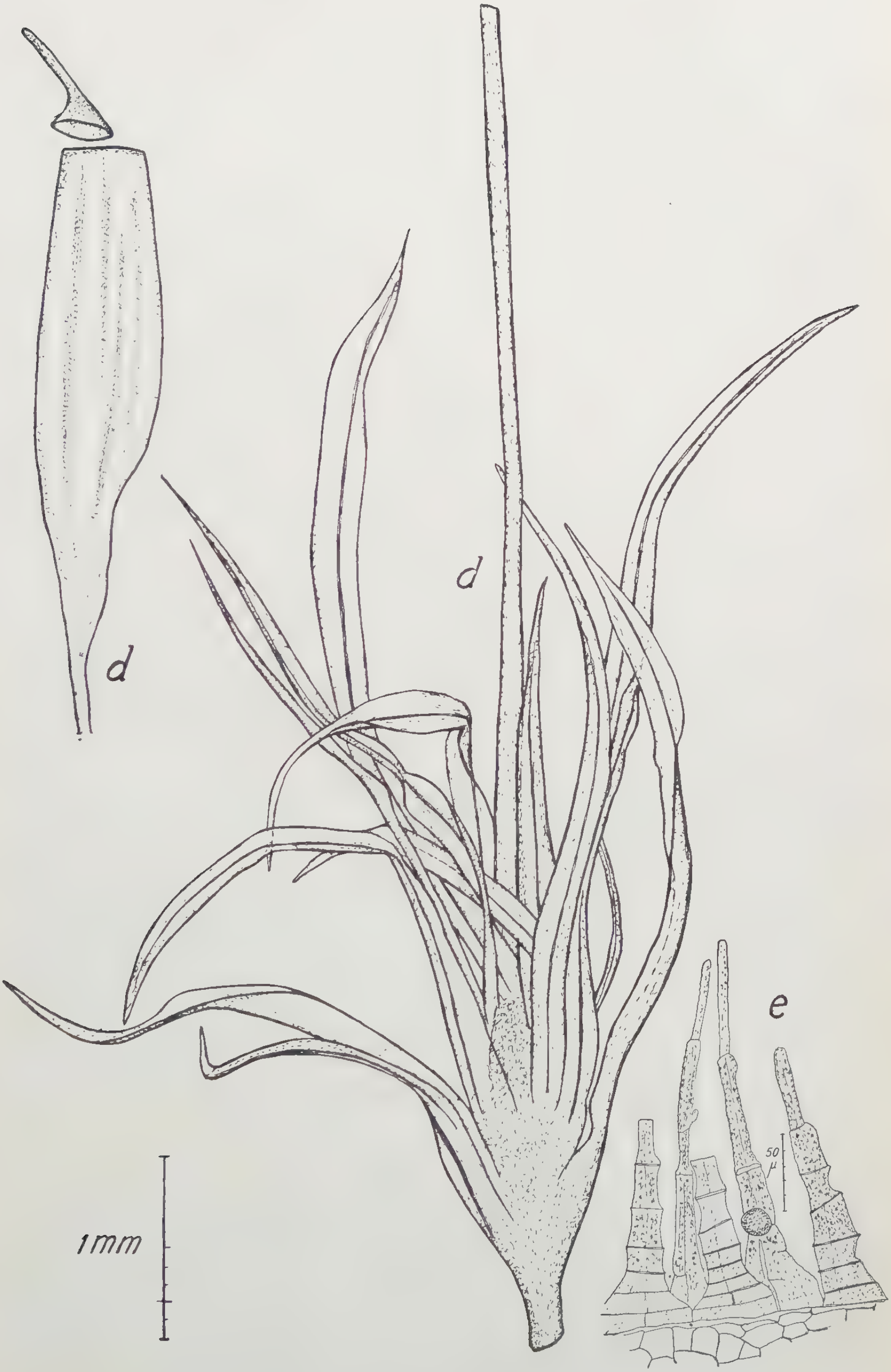

PLATE IX *(Continued)*
Explanation see next page

using the misleading specific epithet "sulcatum" as a clue for their determinations.

When we compare the type specimens of *O. sulcatum* with *O. lanceolatum* we should think them quite different, *O. lanceolatum* having short setae and a relatively small capsule (Plate VIII). Further study might support this view, because we found again and again in the collections a bigger and a smaller form. In several richer collections our suspicion has been raised, for we found there the bigger and the smaller sporogonia intermixed in the same tuft (*O. sulcatum* coll. BELL).

These specimens show that the dimensions of the sporogonia are to a certain extent dependent on conditions of local climate and changing weather conditions. The same phenomena is seen in the supposedly homogeneous *O. l. lineare*, in its recent European stations.

The form of the leaves and the breadth of the cells is probably also much influenced by growing conditions. It could not be by accident, that the plants from Masons Falls in Australia have the broadest leaves, but when we compare the type of *O. l. sulcatum* with *O. l. lineare*, *O. australe* ssp *australe* and *O. australe* ssp *robustiusculum* we get the impression that the differences in leaf form are to a certain extent also genotypical.

For a further elucidation of this complex taxon we need culture experiments and ecological observations, in order to investigate if there exist special biotypes with constantly smooth peristome, in contrast with the highly papillose and for a better evaluation of the different leaf types: setaceous (coll. BELL. Plate VIII*a*), narrow lanceolate leaves (type of *O. lanceolatum*) and somewhat broader leaves.

EXAMINED SPECIMENS:

Australia: New Holland, herb. Hooker & herb. Wilson (K & BM).

W. Australia: Swan river, James Drummond no. 263 (BM, holotype; K and NY isotype); Karriforest, 4 miles E. of Pemberton, leg. J. H. Willis, 1947, no. 722; (ex herb. Willis. WM).

N. S. Wales: Port Jackson district, Tempe near Sydney, leg. Hamilton, 1898 (S, NWS, H); Woronora River, leg. E. Cheel, 1901 (NSW, H); Kerosine Bay, 1884, no. 108 (NSW); Double Bay, leg. Whitelegge, 1884 (NSW, H); Ball's Head Bay. Sydney, leg. Whitelegge, 1884 (MEL, isotype of *O. zetterstedtii* C.M.); Wollongang, leg. Watts, 1895 (NSW; H; K as *O. zetterstedtii*); Nellius Glen, Katoomba, Blue Mountains, leg. Whitelegge, 1891 (H, NSW, as *O zetterstedtii*); Nepean river, leg. W. W. Watts, 1899 [K, H; det. as *O. pallens* (Hook.f. et Wils.) Broth. by Brotherus)]; Gosford, leg. Whitelegge, 1891, no. 446 (NSW; H, det. as. *O. pallens* by Brotherus); Mt. Duval, leg. Watts., 1903 (NSW; H, det. *O. pallens* by Brotherus); Lilyvale, leg. Forsyth, 1900, no. 456 (S, NSW).

EXPLANATION OF PLATE IX

O. lineare ssp *sulcatum:*

a. habit (Australia Worona river, leg. CHEEL, NSW).

b. capsule, Australia (Mt. Lofty, leg. OPHEL, herb. BARTRAM).

c. peristome (*O. sulcatum*, Karriforest, Pemberton, W. Australia, leg. J. H. WILLIS, 8-9-1947).

d. *O. australe* ssp *robustiusculum* Tasm. leg. WEYMOUTH, no. 2336 Mt. Wellington. St. Crispius, 2000 ft. 28-12-1908, det. BROTH. as *O. sulcatum* Hook.f. et Wils. (NY); habit and capsule.

e. *O. australe* ssp *robustiusculum*, peristome (leg. TAYLOR herb. S).

Victoria: leg. Flora M. Campbell, no. 754 (H); Old Grampians, leg. F. Müller, 1881 (BM), leg. Sullivan, 1887 (MEL& NSW; H), leg. Jos. Tilden, Dec. 1912 (herb. Bartram; NSW); Healesville, leg. Mardock. 1903 (BM); Mason's fall, Kinglake Nat. Park, leg. Willis, 1951 (herb. Willis, MEL); Russell's Dam, Creswick, leg. Willis, 1951 (herb. Willis, MEL); Mt. William leg. Sullivan, 1883 (PC, det. by C. Müller as *O. zetterstedtii* C.M.); Mt. Wellington, Gippsland, leg. F. v. Müller, no. 61, 1855 (type of *O. lanceolatum* Mitten, NY; isotype MEL).

South-Australia: Mt. Lofty, leg. Ophel, 32B, 1948 (herb. Bartram); Blewits Spring, Clarendon, leg. Tepper (herb. Willis, MEL).

Tasmania: ?[1] Coll. Archer, W. End rivulet (K, NY); Hobart rivulet 550 ft, leg. Weymouth, 1898 (BM); Huton, Glaciers Bay, leg. Weymouth no. 2928, 1892 (BM); Lady Edeline Falls, leg. Weymouth no. 2320 (det. Broth., H) Hobart rivulet, Track on wood., leg. Weymouth, no. 208, 1890 (NY, no. 298; H). Near Watson's Skye, leg. Weymouth, no. 1296, 1892 (H); Mt. Faulkner, leg. Weymouth 1892 (S, BM, NSW); N. W. Coast, on rocky bank, Castra Road, leg. Weymouth, no. 2289, 1907 (H); Beaconsfield, leg. Weymouth, no. 1133, 1892 (BM, H, det. as *O. pallens* by Brotherus).

New Zealand: Hokitika, Westland, 1938, leg. Martin no. 318.2 (WM); Riverton rocks, leg. Martin 318.18, 1950 (WM ex herb. M); Port Williams, NZ, Dr Lyall (NY, BM).

N. Island: S. end of S. Rotorua, leg. Allison & Sainsbury, no. 659 (BM); Rotorua, near edge of lake, leg. Allison no. 433, 1930 (herb. Sainsbury), 1929 (WELT); Hawkes Bay, Ohu, security mile Bush, leg. Naylor Beckett, no. 886, 1899 (PC, S, H, K), Rotomabana, leg. Berggren, 1874 (S); Whakapapa, Mt. Ruapeku, 3700 ft, leg. Sainsbury, no. 4066, 1929 (herb. Sainsb.); Eastbourne, Wellington, leg. Martin no. 318.17, 1945 (WM ex herb. Martin).

S. Island: Ravensbourne, Dunedin, leg. Martin, 1880 no. 54 (BM); Pine Hill leg. Bell, collections from Oct. 1886, no. 280, 280*b*; Dec. 1886, no. 1400, 30*b*; Jan. 1887, no. 1000; Febr. 1888 (H); Pine Hill leg. Martin, no. 659, 1948 (herb. Sainsb. no. 11835); Signal Hill, Dunedin, Otago, leg. K. W. Allison no. 94, 1944 (herb. Sainsb. no. 11044); Track to Coverham, Kaikoura ranges, Marlborough, leg. Sainsbury, no. 4067 (herb. Sainsb.); Leith valley, nr. Dunedin, leg. Naylor Beckett, no. 525 (H, herb. Wellington, special form, narrowly related to *O. australe*).

Stewart Island: Collections made by W. M. Martin, in herb. Martin and herb. WM: Thale, 1946 (herb. Sainsb. no. 11047), Kaipipitrack, Paterson's Inlet, 1946, no. 318.5; stream, Ferndale, 1946, 318.6; Pt. Pegasus, Wilson's Bay, peaty coastal bank, no. 318.10, 1949; South of Pt. Pegasus, in Forest, no. 318.11, 1949; Bathing Beach, Oban, no.'s 318.12, 318.15, 1946; seaward Bush, Invercargill, 318.14, 1946, Coastal bank, Big Glory, 316.16, 1948.

4. **Orthodontium australe** J. D. Hooker & W. Wilson. Musci antarctici, London Journ. of Bot. Vol. III, 1844; type in herb. Wilson (BM).

Apalodium australe (Hooker, fil. et Wils.) Mitten. Musci austro-americani. Journ. Linn. Soc. Bot. 12, 1869.

a. **O. australe** ssp **australe.**

Description:

Autoecious or heteroecious. Growing in dense tufts, with crowded leaves, somewhat curled when dry, erect when wet, gradually pointed, rather small setaceous, with stout nerve. Sporogonia generally on a longer seta (6—20 mm), capsules variable in length and form, the general form is oblong (3,5—4 times as long as broad), but sometimes pyriform. (Plate X). Length of capsule from 1,5 to 2,5 mm. Lid of the same length as in *O. lineare* (0,4—0,5 mm), but somewhat more rostellate.

Peristome generally showing great differences in length of outer peristome teeth and segments of the inner peristome. (segments

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[1] This puzzling specimen bears a distinct papillose peristome.

1,5—2 times longer than the teeth). Outer peristome 130—145 μ in length, inner 180—290 μ, both generally pale coloured, both or only the processes papillose.

Spores varying from 12—23 μ. (Plate I 1; II 2*b*; X).

Discussion:

See under *O. australe* ssp *robustiusculum* and *O. lineare* ssp *sulcatum*.

EXAMINED SPECIMENS:

Falkland Islands: Antarct. Exp., 1839—1843, leg. J. D. Hooker (K, holotype; BM; L; S); W. Point Island, leg. Halle 1907, no. 575 (PC, S).

Hermite Island, Cape Horn: Antarctic Exp., 1839—1843, leg. J. D. Hooker, 1841 (K, BM, L, paratype).

Fuegia: Exp. Fennica, leg. Roivainen, 1928—1929 (herb. Bartram). From the following localities: Estançio Carmen, Puesto Millaldeo (139); Estançio Cameron (874); Puesto Artaso (918); Rio Bueno; Lago Linch (1405); Lago Fagnano (254); Rio Rusfin. Expedition Suecia, 1907—1909, leg. Halle & Skottsberg, in herb. S. et herb. PC (det. Cardot): Vallée du Rio Azopardo, 300 m.s.m. (493); Same place, Rio mascarella (494); Almirantazza, Puesto Gomez (495); Cami et Descado (var. *brevisetum* Cardot) no. 496; canal Jeronimo, var. *sinuosifolium* Card. nov. var. (497).

Patagonia: Princeton Sc. Exp. 1896—97 leg. Hatcher (NY; herb. Bartram).

Chile: Punta Arenas, leg. Thaxter, 1905—06, no. 124 (US, FH) and no. 127 (US).

Tasmania: Kangeroo bottom, Sept. 3, 1840, leg. J. D. Hooker (K, BM); Oldfield 330, Brown river; Oldfield 225, 134*b*, Back river (K, BM); Mt. Wellington 2000 ft. leg. J. D. Hooker 1328 (K), St. Crispius track, leg. Weymouth, no. 1149, 1888 (H somewhat intermediate between *O. sulcatum* and *O. australe*), no. 776, 1891 (H, PC); Bush, N.W. of new reservoir, Hobart, leg. Weymouth (MEL); Guy Hawkes Rivulet near Hobart, leg. Weymouth, no. 387, 1890, (H); Batess Creek, Peppermint Bay, leg. Weymouth no. 232, 1889 (H); Balfes Hill, Crador, Huon, leg. Weymouth, no. 157, 1889 (H).

b. **Orthodontium australe** Hook.f. et Wils. ssp **robustiusculum** (C.M.) Meijer comb. nov.

Orthodontium robustiusculum C. M. Symbolae ad Bryol. Australiae II, Hedwigia, 37: 76—171, 1898; Lectotype in herb. H.

Description:

Autoecious or heteroecious. Tufts of a somewhat looser texture than in *O. australe* ssp *australe*, leaves somewhat broader. Seta in many cases much larger (till 26 mm) as well as the capsules (3.2 × 1.0, maximum).

Outer peristome teeth more generally as long as the inner, usually brownish coloured, slightly papillose, inner peristome lighter coloured, more distinctly papillose, segments on a distinct basal membrane, of 2—3 cells in height, sometimes slightly split at their base.

Lid longer than in *O. australe* ssp *australe* (ca. 0,7 mm). (Plate I 2; II 3c; IX).

Discussion:

This form can be distinguished from *O. lineare* ssp *sulcatum* by its generally larger sporogonia, longer setae (10—26 mm) and larger capsules. The maximum dimensions of sporogonium of *O. sulcatum* are the minimum dimension in *O. robustiusculum.* The maximum length of the peristome teeth is somewhat larger, but the whole structure is rather similar in both. It is this form which has caused very much confusion among bryologists. We find specimens belonging to *O. australe* ssp *robustiusculum* named as *O. sulcatum, O. lanceolatum* and *O. australe*, by BROTHERUS and WEYMOUTH and when we compare them, we cannot see any real differences. CARL MÜLLER (1898) selected one of them and described it as his new species: *O. robustiusculum.* This was totally neglected by other bryologists, perhaps because they had the suspicion that this was yet another of CARL MÜLLER's species without any real existance in nature.

A good illustration of the difficulties in a preliminary study in this group is given by the following extract from DIXON's generally praised "Studies in the Bryology of New Zealand" (1926) p. 197:

> "*Orthodontium sulcatum* Hook. f. et Wils.
>
> The only species. Recognized at once by the long narrow linear setaceous leaves, erect, elliptic capsule, sulcate when dry and empty, the rostellate lid, and delicate peristome.
>
> I have it from two or three stations in the South Island, but it would seem to be rare. It is also found in Australia and Tasmania. I strongly suspect that *O. sulcatum* will have to be reduced to *O. australe* H. f. & W. Lond. Journ. Bot. iii, 545 (1844), from the Falkland Islands, Hermite Island and Tasmania. The authors of the two species did not think it necessary to compare them with another, no doubt since in their view *O. sulcatum* differs from all the other species in the furrowed capsule while *O. australe* is figured (and described by implication) as with smooth capsule. I have examined the types of both species and if the matter could rest on these alone the two might well stand, but the matter is quite altered when other specimens are examined. In the original specimens of *O. australe* from the Falkland Islands, the young capsules are quite smooth, while the old ones are irregularly plicate, but do not show any trace of the regular ribbing that is characteristic of *O. sulcatum.* There are however, few or no capsules in good condition."

We have seen that the ribbing of the mature sporogonia occurs in all the species of the subsection Linearis and that it therefore cannot be used for distinguishing species within this section. Juvenile states differ from mature. DIXON proceeds as follows:

> "Tasmanian specimens in HOOKER's collection are very puzzling, and perhaps the best comment on the distinctness of the two plants is to be found in the fact that in herb. HOOKER there are certain specimens labelled *O. sulcatum* which certainly belong to *O. australe* and others labelled *O. australe,* which if the two are to be kept separate must as certainly be referred to *O. sulcatum.* The capsules in fact seem to show all gradations from a smooth

> surface to a very regularly ribbed and sulcate one. The bulk of the specimens however lack capsules in good mature condition and I do not think the problem can be solved satisfactorily except by study of good material in the field".

From this it appears that DIXON was not quite sure about the worth of the ribbing as a character and from the last sentence we conclude that he was not quite sure of his own concept of both species. That he did not succeed in finding the real differences, owing to lack of material, appears from what follows:

> "*O. sulcatum* is described and figured as with short only slightly tapering leaves, but this is not a constant character. Tasmanian specimens of ARCHER's collecting with highly ribbed capsules, have the leaves very narrowly and long tapering, which is the case also with New Zealand specimens in herb. Kew, coll. NORKETT".

These observations are right, as will be shown later. MITTEN brought ARCHER's collection in his *O. lanceolatum*. DIXON continues:

> "RODWAY, (Tasmanian Bryophyta, Mosses) described both *O. australe* and *O. sulcatum* as with sulcate capsules, separating them by the form of the fruit, oblong in the former, pyriform in the latter, but there is no difference in the form of the capsule, either as figured by HOOKER or as exhibited by the original specimens, except in as much as is produced by different stages of maturity".

To a certain extent we agree with this opinion, but our observations revealed a slight tendency for more oblong capsules among *O. australe* and showed that all old sporogonia may be distinctly furrowed.

So much for the earlier difficulties in recognizing *O. australe* ssp *robustiusculum*. The differences between *O. lineare* ssp *sulcatum* and *O. australe robustiusculum* are mainly in the dimensions of the sporogonia, setae etc. as we showed earlier. The question then arises whether the former taxon cannot be a haploid state of the latter. The dimensions of the sporogonia suggested investigation of this possibility. It turned out then that the real differences in size of the sporogonia are not correlated with considerable difference in the diameter of the spores. They measure 11—20 μ at *O. lineare* ssp *sulcatum* and 15—24 μ at *O. australe* ssp *robustiusculum.*

Moreover the leaf cells do not differ considerably: average breadth of cells in the middle of the leaf in *O. l. sulcatum* 9—14 μ, in *O. robustiusculum* 10—12 μ.

Another explanation, at first sight more fantastic, but after longer consideration more likely, is that hybridization of *O. australe* and *O. lineare* ssp *sulcatum* has taken place in Tasmania. In these autoecious groups of mosses one cross is enough to give rise to quite a new homozygous "race" (LOTSY 1928).

We remember in this connection the rather robust, small-leaved

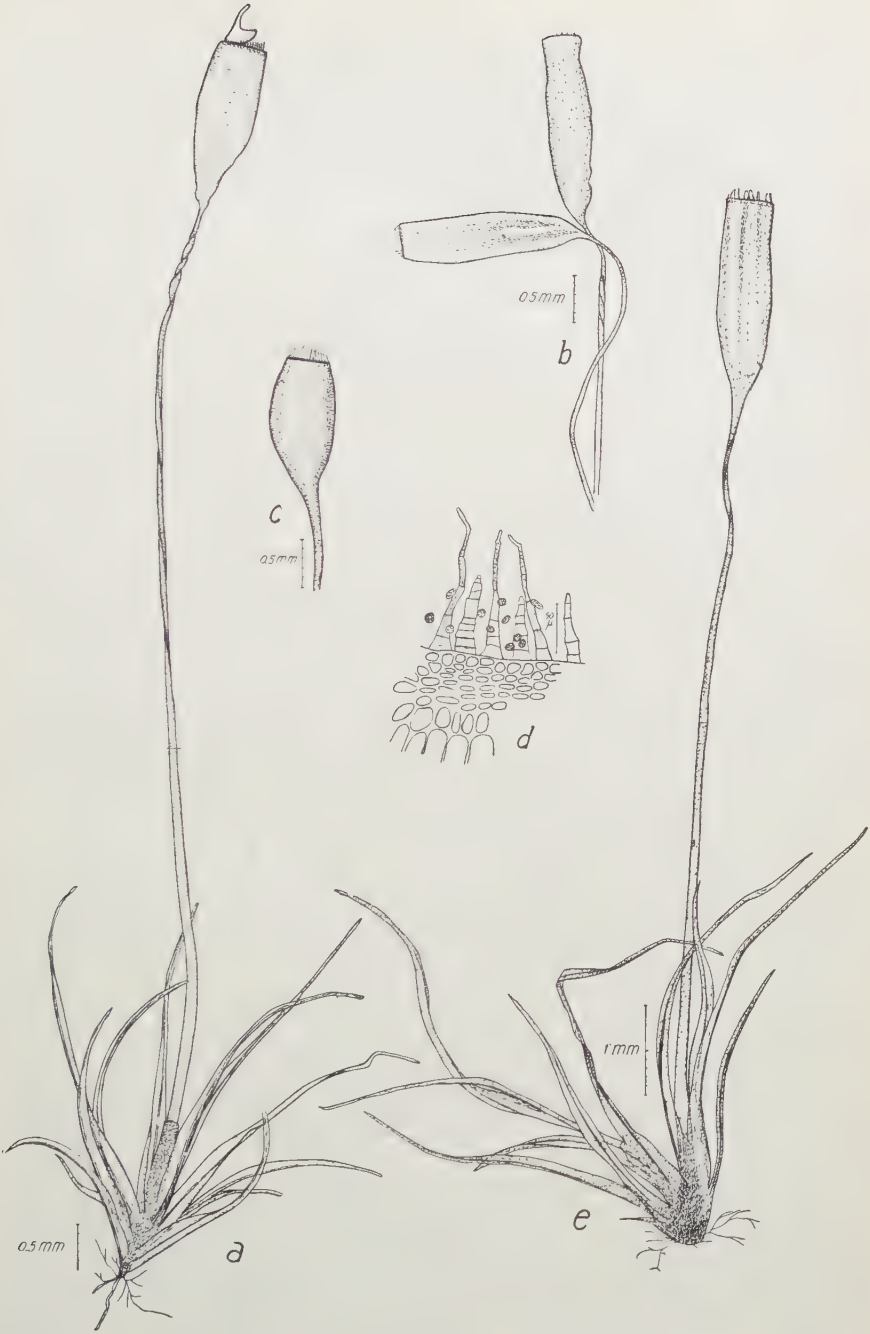


PLATE X

a. *O. australe.* Isotype (NY).
b. *O. australe,* old sulcate capsules. Patagonia. Princeton Exp. coll. Hatcher (NY).
c. *O. australe.* Leg. Roivanen, Fuegia media; Estancia Carmen 18-1-1929. (More or less pyriformous capsule, herb. Bartram).
d. Peristome, *O. australe* (isotype; NY).
e. *O. australe* × *O. sulcatum*?? Leg. Archer, Tasm. (NY).

"*O. lanceolatum*" from Tasmania (coll. ARCHER). Its more papillose peristome and longer setae might be characters introduced from *O. a. australe* into *O. lineare sulcatum* and the lack of difference in spore size and cell size would thus be explained.

By such hybridization the origin of the puzzling narrow-leaved forms with short small sporogonia, formerly included in *O. lanceolatum*, from Lady Edeline Falls, Tasm. and *O. sulcatum* coll. BELL. Pine Hill Nw Zealand, Plate VIII, could also be explained.

It appears from these considerations that our chief need is for more collections and more ecological information, in short, for more field knowledge. Our taxonomical conclusions should then be checked by cytological and genetical investigations.

EXAMINED SPECIMENS:

Tasmania: Eagle Hawk Neck Hill, East Coast, 1889, leg. Weymouth (H, lectotype of *O. robustiusculum* C.M.; S); Forestiers Peninsula, leg. Weym. no. 257 (NSW); Mt. Wellington St. Crispius well leg. Bastow, 1886 (NSW), St. Crispius track, leg. Weymouth 1890, no. 320 (NY, H), 1891 (H, PC) 1908 no. 2336 (NY, H, det. Broth. as *O. sulcatum*); Mt. Wellington, leg. Weymouth, no. 1498, 1893 (NY, S, H), Hobart rivulet track, no. 298, 1890, (NY, H), Shady banks 2400 ft, no. 2566, 1896 (H), New track, Vinger Post, no. 1166, 1890 (H, intermediate form between ssp *australe* and ssp *robustiusculum*), Deep Creek, no. 2168, 1897 (H), Derby, 1000 ft, leg. Weymouth, no. 2716, 1913 (H, K); South Coast Recherche, near Leprena, 200 ft, leg. Weym., no. 13, 1911; Gully Mt. Dromedary, leg. Bastow no. 649, 1886 (BM); Hobart water works, leg. Weym., no. 2926, 1891 (BM); Recherche bay, leg. Weymouth, no. 2882, 1911 (H), Recherche, Catamassan, leg. Cockayne & Weymouth, no. 2579, 1911 (H, both with somewhat glossy leaves); East Coast, 1400 ft, leg. Weymouth no. 2477, 1911 (H); Lady Edeline Falls, leg. Weymouth no. 2346, 19-1—1909, (H, no. 2320, 19-1—1909, *O. sulcatum*, from same locality!).

Australia: Vict. Erskine River, leg. W. W. Watts, no. 1077 (H).

New Zealand: Bluff, herb. Bell. (H).

5. **Orthodontium pallens** (Hook.f. et Wils.) Broth. Engler & Prantl.

Weissia pallens (Hook.f. et Wils.). Ic. Plant. Vol. IV, New Series Tab. 739A, 1848; holotype in herb. BM.

Seligeria pallens C.M. Syn. musc., p. 423, 1849.

Microdus pallens Par. Index bryol., p. 805 (1896).

Zygodon lineare Taylor nom. nud. (herb. Mitten, NY).

Apalodium lineare (Taylor) Mitten. Transact. and Proc. Royal Soc. of Victoria, Vol. 19, 1883, non *Apalodium lineare* (Schwaegr.) Mitten, Voy. Challenger Exp. 1885.

Description:

Growing in tufts, or intermixed with other mosses. General habit of gametophyt as *O. sulcatum*. Autoecious. Leaves rather glossy, lanceolate, gradually pointed, upright standing, or somewhat bent, greatest breadth ca. 0,3 mm, length ca. 2—3 mm, cells at middle of leaf ca. 10 μ in breadth.

Seta rather short (ca. 3—4 mm). Capsule somewhat bent, slightly pyriform, with short neck, collenchymatous cells near the margin of the mouth very distinct. Lid oblique rostellate. Peristome rather

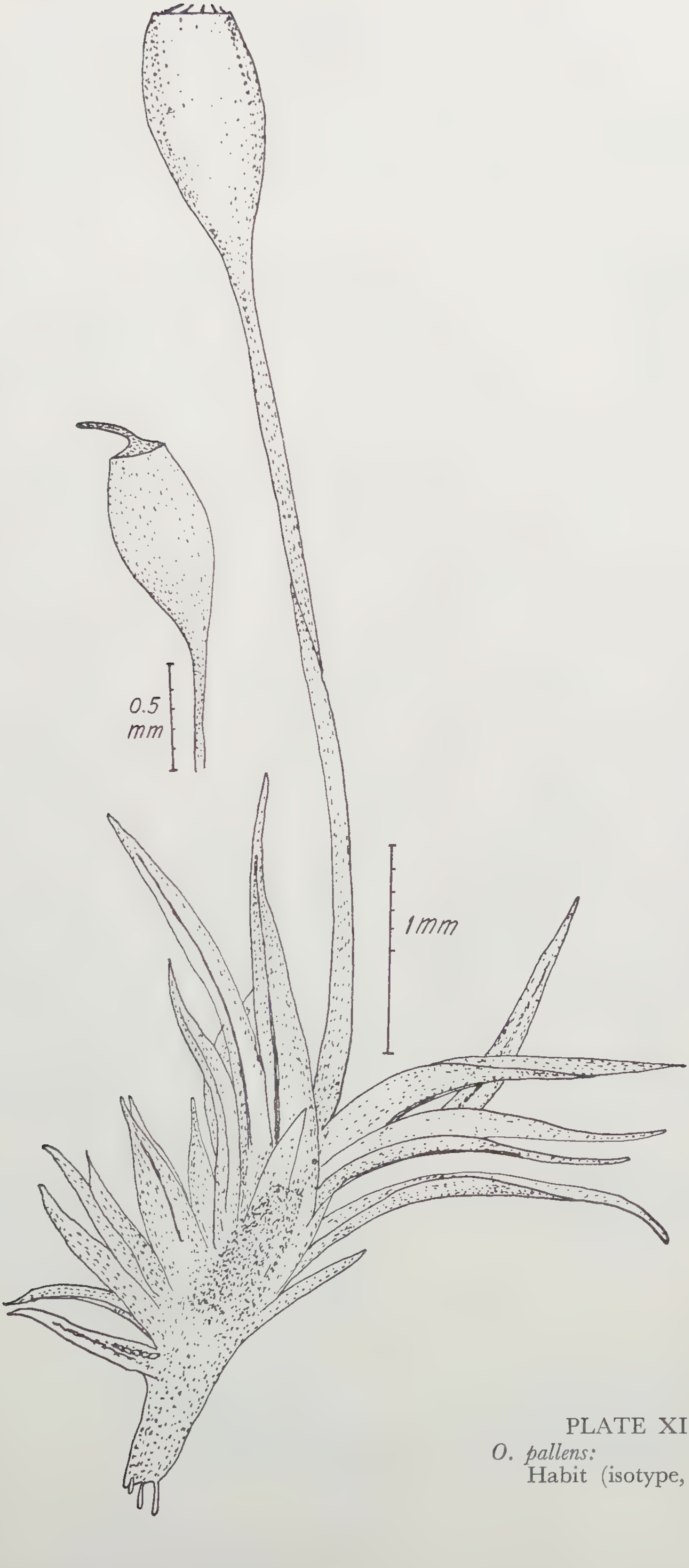


PLATE XI
O. pallens:
Habit (isotype, NY).

rudimentary developped. Outer peristome teeth ca. 110—120 μ long, totally smooth, light yellow, sometimes with irregular sculptures; inner peristome mainly composed of a very undistinct basal membrane, very fragile and thin, translucent, split between the outer teeth. Processes not developped. Spores 20—25 μ, finely punctate (Plate XI).

Discussion:

This species is difficult to distinguish, without sporogonia, from rather broad leaved forms of *O. sulcatum*. It is not surprising that bryologists confused it with juvenile states of *O. sulcatum* and *O. inflatum*, for in both such forms the inner peristome is only slightly developed; in the last named it remains thin and translucent even in the mature state. It is fairly certain that *O. pallens* is narrowly related to *O. inflatum* and to *O. sulcatum*. The large size of its spores is a common feature with *O. inflatum* and the shape of the leaves with *O. sulcatum*. The tendency to produce reduced or rudimentary inner peristomes can be traced within the series leading from *O. pallens* over *O. inflatum* to *O. infractum*. *O. pallens* forms a bridge between subsection *Linearis* and subsection *Pellucens*.

EXAMINED SPECIMENS:

S. W. Australia: Swan River, leg. Drummond, no. 201 (BM type; K; NY, mixed with the type of *O. sulcatum* Hook.f. et Wils.!).

Tasmania: South Coast Recherche, forest near Deprena, 200 ft., leg. Weymouth, 1911 (NY, mixed with *O. robustiusculum*).

6. **Orthodontium inflatum** (Mitt.) Par. Index bryol. 1894—1900.

Apalodium inflatum Mitten. Voy. H. M. S. Challenger, 1885; holotype in herb. NY.

Orthodontium ovale C.M. ex Broth. Some new species of Australian mosses described. II, Öfversigt af Finska, Vetenskaps-Soc. Förhandl. 35, 1892—1893, Helsingf. 1893; lectotype in herb. H.

Wilsoniella compacta Geheeb, nom. nud. Watts & Whitelegge 1905. Cens. Musc. Austral. Proc. Linn. Soc. of NSW.

O. pallens (Hook.f. et Wils.) Broth. sensu Brotherus, Engler & Prantl., is partly *O. inflatum*, partly *O. lineare* ssp *sulcatum*, according to the specimens and determinations of Brotherus in herb. H.

Description:

Autoecious. Very densely growing in tufts. Plants with many rhizoids at their bases. Leaves somewhat glossy, very narrow lance-

EXPLANATION OF PLATE XII

O. inflatum:

a. Habit (type mat.; NY).
b. Young capsule with calyptra (type mat. of *O. ovale* C.M., NSW).
c. Capsule with lid.
d. Peristome (type mat. of *O. ovale*; NSW).

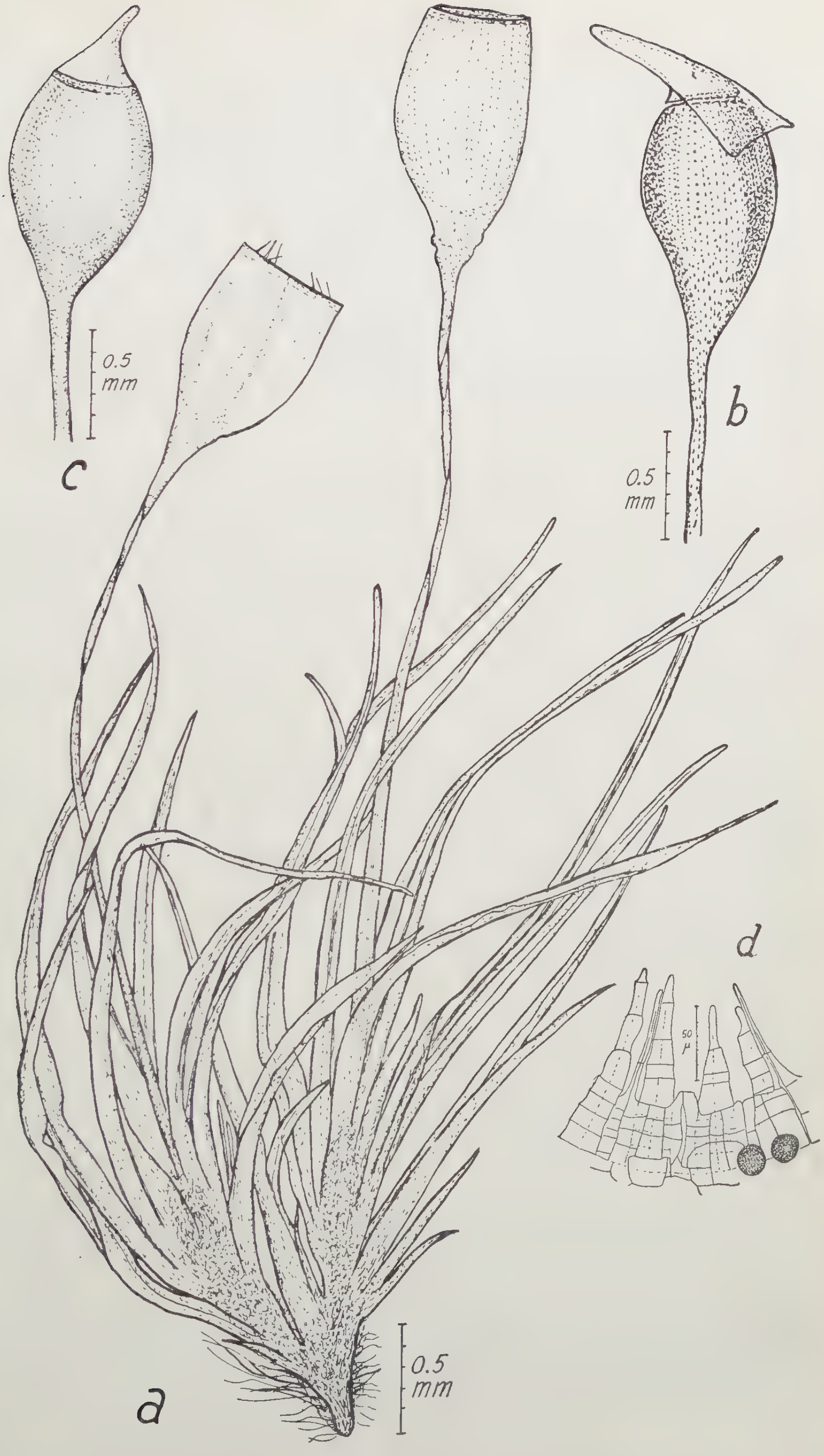


PLATE XII

olate, gradually acuminate in a long point. Maximal breadth ca. 0,20—0,30 mm, max. length 3—5 mm. Cells prosenchymatous, breadth c. 8—10 μ, nerve very distinct, relatively broad, till 1/4 of leaf breadth. Seta 4—5 mm, capsule erect or only slightly bent, when ripe distinctly broadly pyriform (swollen), c. 1—1,2 mm long and 0,6—0,7 mm broad, occasionally with some broad furrows. Neck relatively short. Lid rostrate, length one third of total capsule length. Calyptra longer than the lid, cucullate. Outer peristome well developed, yellow-brown coloured. Inner peristome with a rather high thin and translucent basal membrane, composed of 3—4 cells in height, with very fragile narrow processes and with a median line, which becomes indistinct below the apex. Spores 20—30 μ, in diam. (Plate XII).

Discussion:

O. inflatum is very easy to recognize by its combination of narrow leaves, swollen sporogonia, long lid, big spores and the rather translucent inner peristome. Juvenile states are sometimes wrongly named *O. sulcatum* or *O. pallens*. This species is the closest relative of the indo-malayan *O. infractum*. They possess the long lid in common, together with the translucent inner peristome and the more pyriform shape of the capsules. Their greatest difference consists in the shape of their leaves.

EXAMINED SPECIMENS:

Australia, N. S. Wales: Blue Mountains, leg. Rev. R. Collie, 1885, holotype (NY); Botany Bay, La Perouse, leg. Whitelegge 1885 (MEL, det. as *O. ovale* by Brotherus, in herb. H, under the name *Wilsoniella compacta* Geheeb nom. nud., no. 211, leg. Whitelegge no. 297); La Perouse leg. Forsyth 1898 no. 3960 (NSW, det. as *O. pallens* (Hook.f. et Wils.) Broth. by Brotherus in herb. S), 1899 (H, no. 644, det. as *O. ovale* by Broth; PC), 1900. [H, PC, as *O. lineare* (Mitt.), herb. Cardot = *O. pallens* comm. Broth]. *It is very probable that Forsyth made these collections all at the same locality. They obtained four different wrong names*! *Watts and Whitelegge* (1905) *wrote already "may be O. inflatum"*; Pennshurt, leg. Forsyth, no. 954 (NSW, det. Broth: *O. pallens*); Gosford, leg. Whitelegge no. 445, 1891. The type coll. of *O. ovale* C.M. ex Broth (NSW; H, lectotype; PC); Tempe near Sydney, leg. Forsyth, no. 541, 1899 (det. Broth: *O. ovale*, NSW, H); Port Jackson district, leg. Forsyth 1898 (comm. Brotherus *O. ovale* C.M., S, H); Bollina, Sydney, Cook's river, leg. W. W. Watts, no. 128, 1896 (det. Broth: *O. ovale*, H, PC); Park Grays Island, leg. Watts, 1896 (H, det. Broth: *O. ovale;* BM; WM ex MEL); Watsons Bay, leg. Hamilton, leg. Watts. no. 128 (H).

S. E. Vict: Stanley Creek, leg. J. H. Willis, 1951, (det. G. O. K. Sainsbury as *O. sulcatum*, WM ex herb. MEL).

7. **Orthodontium infractum** Dozy & Molkenboer. Musci frond. Arch. Ind. Ann. Sciences, Nat. 1844, p. 313; Musci frond. ex Arch. Ind. 1844. With plate; type in herb. L.

Orthodontium brevicollum Fleischer. Die Musci der Flora von Buitenzorg II Bd.: 495, 1902—1904. With figure; type in herb. Fleischer, FH.

O. sulcatum (Hook.f.) et Wils. p.p. C. M. Synopsis Muscorum, 1849, p. 239.

Description:

Autoecious, growing in tufts. Plants densely leaved; leaves with the same metallic gloss as the leaves of *O. pellucens*, dry somewhat curled, wet curved, gradually pointed, keeled, variable in breadth (0,35—0,45 mm) and in length (2—5 mm); margin undulated on some places, occasionally slightly denticulate near apex. Cells narrow prosenchymatous, c. 6—10 μ in breadth and 10—15 times as long as broad, towards the basis wider (as in all Orthodontium species). Nerve possessing stereid cells. Seta 5—12 mm in length. Capsules erect or somewhat bent, ovato-oblong or pyriform, c. 1 mm long; cells near margin of capsule of the ordinary collenchymatous type; lid rostrate, $^2/_3$ of total capsule length. Outer peristome yellow ochre, smooth, inner with translucent basal membrane, some cells high. Processes narrow, generally darker coloured than the basal membrane, median line not fully developed. Spores minutely punctate, 14—18 μ in diam. (Plate II e; XIII.)

Discussion:

O. infractum is standing at the borderline of the group of species which are closely related with *O. pellucens.*

It differs from that species in its smaller dimensions, narrower cells and its less developped inner peristome. Pyriformous capsules, with long lids occur also within the range of *O. pellucens. O. infractum* is not so very easy to distinguish from *O. novae-guineae.* The last species possesses however longer setae, somewhat greater leaves, and a less pyriform capsule. It has a well developed peristome, inner and outer are papillose at maturity. FLEISCHER described *O. brevicollum* as a subspecies from the same area as *O. infractum.* The types of both differ indeed as regards shape of the capsules and of the leaves, the capsules being more pyriformous and the leaves broader in *O. brevicollum.* The other collections show however that these are not constant differences. In some instances, forms with the typical characters of both intergrade within one tuft. That's why we put together here such minor variants in one species.

EXAMINED SPECIMENS:

Java: Type collection, leg. Zippelius Sederatoe, Java (L); coll. Horsfield 73 and 13, herb. Mitten (NY); Pangerango leg. Nyman, 1898 (L); Pangerango, 2700 m, leg. Fleischer 1898 (type coll. of *O. brevicollum*, L; PC, H); Dieengplateau, Praoe, 2500 m, leg. Fleischer, 1898 (S, L. H), 1901 (S, L, NY) Papandajan, leg. Verdoorn 1930, det. Dixon (BM), leg. Wichura, no. 2496, 1861 (H); Pancoban Prau, leg. Wichura, no. 2498, 1861 (H); Pangerango, leg. Wichura 24976 and 249760, 1861 (H).

Ceylon: Hotton-plaines, 2500 m, leg. Fleischer, det. as *O. brevicollum* (L); leg. Binstead, 1913 (BM); Central Province leg. Thwaites, no. 102 (NY, BM, MEL); Ambewelle-Pattipola, 1900 m, leg. Herzog, 1906 (H).

Borneo: leg. Korthals (L, S).

8a. **Orthodontium pellucens** (Hooker) Br. & Sch. Bryol. Eur. fasc. 3—4, 1844.

Bryum pellucens Hook. Ic. pl. rar. 1, t. 34, 1837; holotype in herb. K.

Apalodium pellucens (Hook.) Mitt. J. Linn. Soc. Bot. Vol. 12, p. 238, 1869.

Orthodontium confine Hampe. Ann. Sc. Nat. 5. ser. 4: 338, 1865; holotype in herb. BM.

Apalodium confine (Hampe) Mitt. Voy. H. M. S. Challenger, 1885.

Orthodontium fendleri C. M. Linnaea 42: 473, 1878—79; (N.F. Bd. VIII, no. 33); lectotype in herb. N.Y.

Orthodontium ulei C.M. Bull. Herb. Boissier 6: 29, 1898; lectotype in herb. NY.

Orthodontium pycnoblastum C.M. nom. nud. (herb. name of the type of *O. ulei* C.M.).

Orthodontium arenarium C.M. Bull. Herb. Boissier 6: 29, 1898; lectotype in herb. NY.

Stableria gracilis (Schwaegr.) Lindb. var. *californica* Howe, Erythea Vol. 5: 92, 1897; type in herb. US.

Orthodontium gaumei Allorge et Thériot. Rev. Bryol. 1931: T. IV: 194—196.

Description:

Autoecious, growing in loose or very dense tufts, sometimes strongly interwoven with tomentum. Plants 0,5—5 cm high, with a metallic sheen; leaves broader than in most specimens of *O. lineare* and *O. gracile*, 0,3—0,5 mm broad and 3—6 mm long, twisted when dry, acute or acuminate, usually rather short compared with other species, with occasional teeth near the apex, cell walls rather thick, cells in the midst of the leaf 13—18 μ broad, linear oblong.

Sporogonia with red setae, 5—8 (7—14) mm long, capsule red-brown, erect-flexed, gradually tapering into the neck, at mouth rather broad (0,50—0,65 mm), 2—3 times as long as broad, (max. length 1,85 mm min. 0,80 mm). Older capsules regularly furrowed when dry, with distinct dark border of collenchymatous cells near the margin.

Peristome rather robust but variable, outer teeth 200—290 μ, segments of the inner peristome 150—300 μ, the latter with splits at base, along the median line. Outer teeth somewhat broader at base than the processes (± 30 and 20 μ respectively), outer teeth of 8—12 joints, (*O. gracile* 6—9), processes 6—7. In fully developed peristome the outer teeth are reddish brown in colour and densely papillose, papillae sometimes in indistinct rows, the inher teeth are lighter coloured. In unripe capsules the peristome is almost smooth and paler coloured, segments on thin basal membrane, 3—4 cells high.

EXPLANATION OF PLATE XIII

O. infractum:

a. Habit (isotype material of *O. brevicollum* Fleisch; L).

b. Young capsule (coll. FLEISCHER, 363, Dieeng plateau, Praoe, herb. L.).

c. Pyriformous and lanceolate capsule from coll. HERZOG, Ceylon. Pattipola-Ambevelle (herb. H).

d. Peristome (coll. FLEISCHER, Dieeng, Praoe, Java (L).

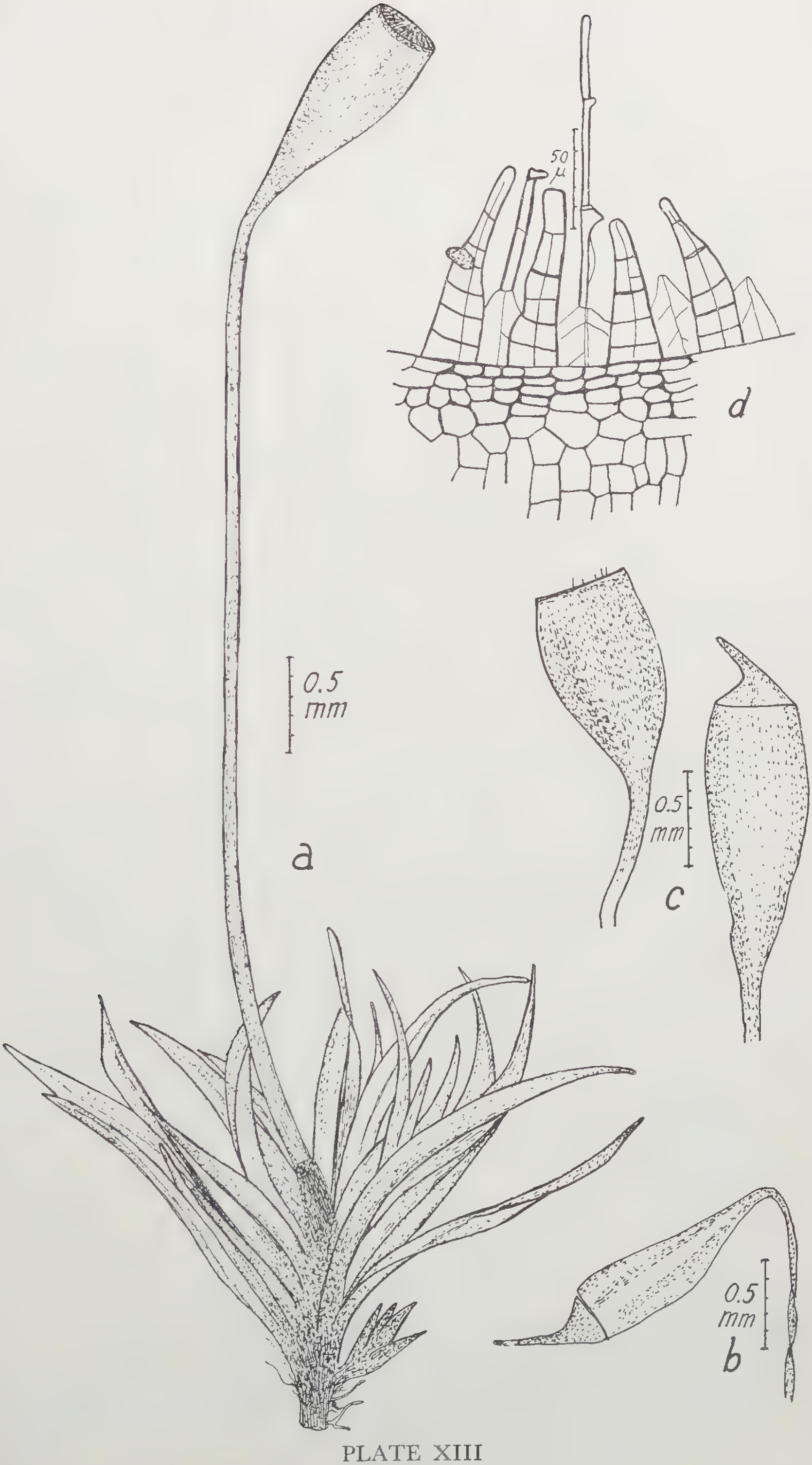


PLATE XIII

Lid rostrate, often oblique, usually ± 0,75 mm long, rarely 0,80 mm. Spores finely punctate dark brown, 15—20 μ. (Plate II 2e; XIV).

Discussion:

O. pellucens s.s. is a widely distributed species along the South American Andes. Very slightly different, or quite identical forms of this species have been described as separate species: *O. confine*, *O. fendleri*, *O. ulei*, *O. arenarium*. Mrs. BRITTON indicated already on the sheets of the New York herbarium that her studies on this group resulted in a putting together of these forms. LE ROY ANDREWS (1932, 1935) paid attention to these studies. I have tried to find any differences of which I could suppose that they were not due to phaenotypical variation, but I could not succeed in finding them.

There exists however one remarkable form, which is not described as a separate taxon, namely the form from Jamaica. It has shorter setae and a more pyriformous capsule. Most of the Jamaica collections have this aberrant aspect. (Table XIV*c*).

In the list of synonyms has also been put *O. gaumei* Allorge & Thériot. Some twenty years ago that form has been detected in France (GAUME, 1932), and afterwards in Spain (ALLORGE, 1934). It was repeatedly compared with *O. infractum* Dozy & Molkenboer, by the authors, by MARGADANT & MEIJER (1950) and previously by REIMERS (1941). The last author supposed that it could be more closely related to *O. pellucens* (Hook.) Br. eur., but MARGADANT & MEIJER (1950) uttered some doubts against the geographical argument used by REIMERS for his statement.

A closier comparison showed me distinctly that REIMERS was right. The leaf types are just the same. I made drawings of *O. pellucens* (*O. confine* type) and *O. gaumei* type, which showed the very great resemblance. The resemblance with *O. infractum* is only apparent, because the sporogonia were young. In such a state the lid can be rather long in comparison with the theca.

The peristome fragments which I saw were smooth, but Mr. POTIER DE LA VARDE kindly informed me that he had a sample for study which had them distinctly papillose.

In this way the words of ALLORGE & THÉRIOT (1931) become even more true: "La présence d'un Orthodontium à Fontainebleau constitue un fait bryogéographique tout à fait intéressant; elle ajoute un cas remarquable aux disjonctions déjà connues dans la flore muscinale de l'Europe (ALLORGE 1931)."

EXPLANATION OF PLATE XIV

O. pellucens:

a. Habit. Coll. LINDIG, Nova Granata. Monte de Moro (L).
b. Capsule (isotype of *O. confine* Hampe, L).
c. Pyriformous capsule, Jamaica, herb. MITTEN (NY).
d. Peristome. Jamaica, Coll. E. G. BRITTON, New Haven Gap, no. 65 (NY).
e. Apex of leaf (type material of *O. gaumei;* PC).

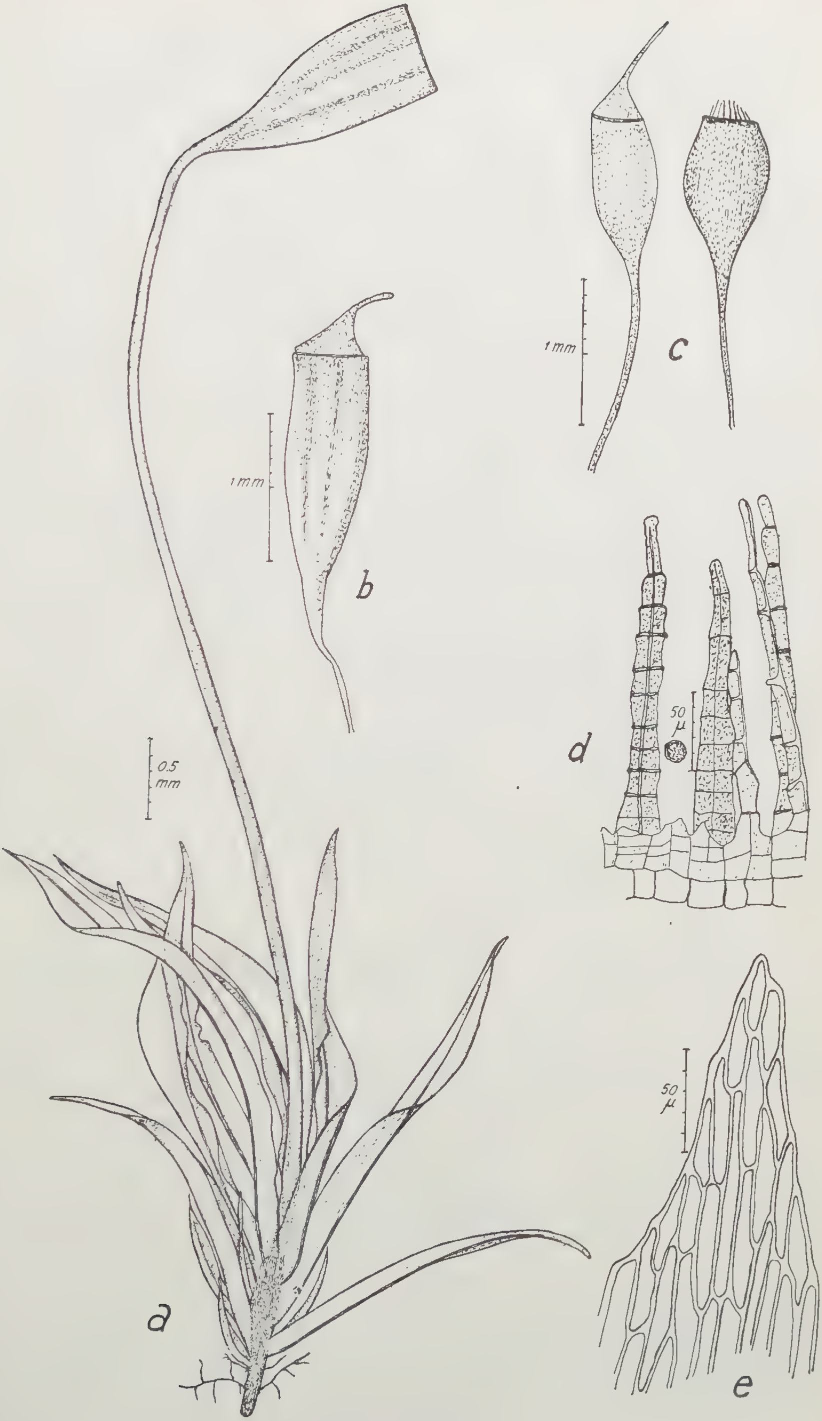


PLATE XIV

Examined specimens:

California: Eureka, on redwood stumps, leg. Howe, 1896 (U.S.).

Tennessee: Sevier Co., 3800 ft, leg. A. J. Sharp, no. 34713, 1934 (NY, same place 1937, herb. Bartram).

Cuba: Loma del Gato, leg. Clement. (NY; PC, det. as *O. arenarium* C.M. by Thériot).

Haiti: Mornes de la Hotte, leg. Ekman, 1918, no. 565, det. Thériot as *O. osculatianum* (BM; NSW; U.S.).

Jamaica: Vicinity of Cinchoma, New Haven Gap, leg. E. G. Britton, 1906 (NY); Hark 1883, herb. Mitten (NY); Morces Gap, leg. G. E. Nichols, no. 44, 1906 (NY, S).

Guatemala: Dept. Quezaltenango, Volcan Zunil, 2500—3800 m, leg. Steyermark, 1940 (herb. Bartram).

Costarica: La Palma, 1500 m, leg. Valerio, no. 137, no. 138, 1928 (NY. herb. Bartram); La Fuenta, Peratta, 1200 m, leg. Alfaro, no. 22, 1934 (herb. Bartram); Volcan de Barba, 2400 m, 1926 (herb. Bartram); El Silencio de San Remon, leg. Breues, 1933 (herb. Bartram); El Gallito, Prov. of Heredia, 2000 m, leg. Valerio, no. 197, 1928, (herb. Bartram; U.S.).

Venezuela: Tovar, leg. Fendler 1854—55, Musci Ven. det. C. Muller, no. 33 (lectotype of *O. fendleri*, NY; S; PC).

Colombia: Surrucucho near Cuenca, leg. Jameson (BM, holotype; NY); Andes Bogotensis, leg. Weir, 6800 m, no. 314 (NY, PC); Dept. Cundinamarca, Parama de Guarca, ca. 3250 m, leg. E. P. Killip, no. 36060, 1939 (herb. Bartram; FH; U.S.); Dept. Tolima, Quindio Highway, 3300—3600 m, leg. Killip, no. 34599, 1939 (herb. Bartram; U.S.); leg. J. C. Mutis, 1760—1808, no. 3383, det. Bartram (U.S.); Bogota, 2500 m, leg. Lindig, 1863, Tequendama) BM, holotype of *O. confine* Hpe; NY; U.S.; PC; S); Guadalupe, 2900 m, 3100 m, Monte del Moro, 2200 m, leg. Lindig (NY, L).

Galapogos Islands: James Island, leg. Stewart, no. 6000, 1905—1906 (NY).

Peru: Dept. Cuczo, Prov. Pavcartambo, Janamayo, 2000 m, herb. Vargas (herb. Bartram).

Bolivia: Between Tolapampa and Mapiri, 2300 m, leg. Williams, 1901 (NY, H); on decayed wood near Mapiri, leg. Williams 1902 (NY).

Brazil: Rio grande do Sul, Bon Jezus, 900 m, leg. Sehuern, 1942 (herb. Bartram); Prov. S. Catharina, Serra Geral, leg. Ule, 1891, Bryoth. bras. no. 132, (NY, lectotype of *O. ulei* C.M.; L; S; PC; H); Caraça, leg. Ule (NY, lectotype of *O. arenarium* C.M.; PC).

Hawai: Kauai, Kohua ridge, C. 3500 ft, leg. Cranwell, Selling & Skottsberg, no. 4091, 1938 (herb. Bartram).

8b. **Orthodontium denticulatum** Geh. et Hampe. En. Musc. hact. in prov. Bras. Rio de Janeiro et Sao Paulo dect. Flora 64, no. 24: 374, 1881, holotype in herb. BM.

Differing from *O. pellucens* in the smooth peristome, the translucent segments and the regular dentate leaf apex. (Plate XV).

Examined specimens:

Brazil: Prope Apiahy, S. Paulo; leg. Louis Puiggari, no. 902, 1879 (BM, type; NY; L; H); Parana, Rio negro, leg. P. Dusen, 1908, det. Broth. (H); Rio Janeiro, leg. Gardner no. 54 (herb. Bartram).

8c. **Orthodontium longisetum** Hampe. Linn. 32: 129, 1863, type in herb. BM.

Apalodium pellucens (Hook.) Mitten p.p., in Mitten, Journ. of Linn. Soc. 12, 1869.

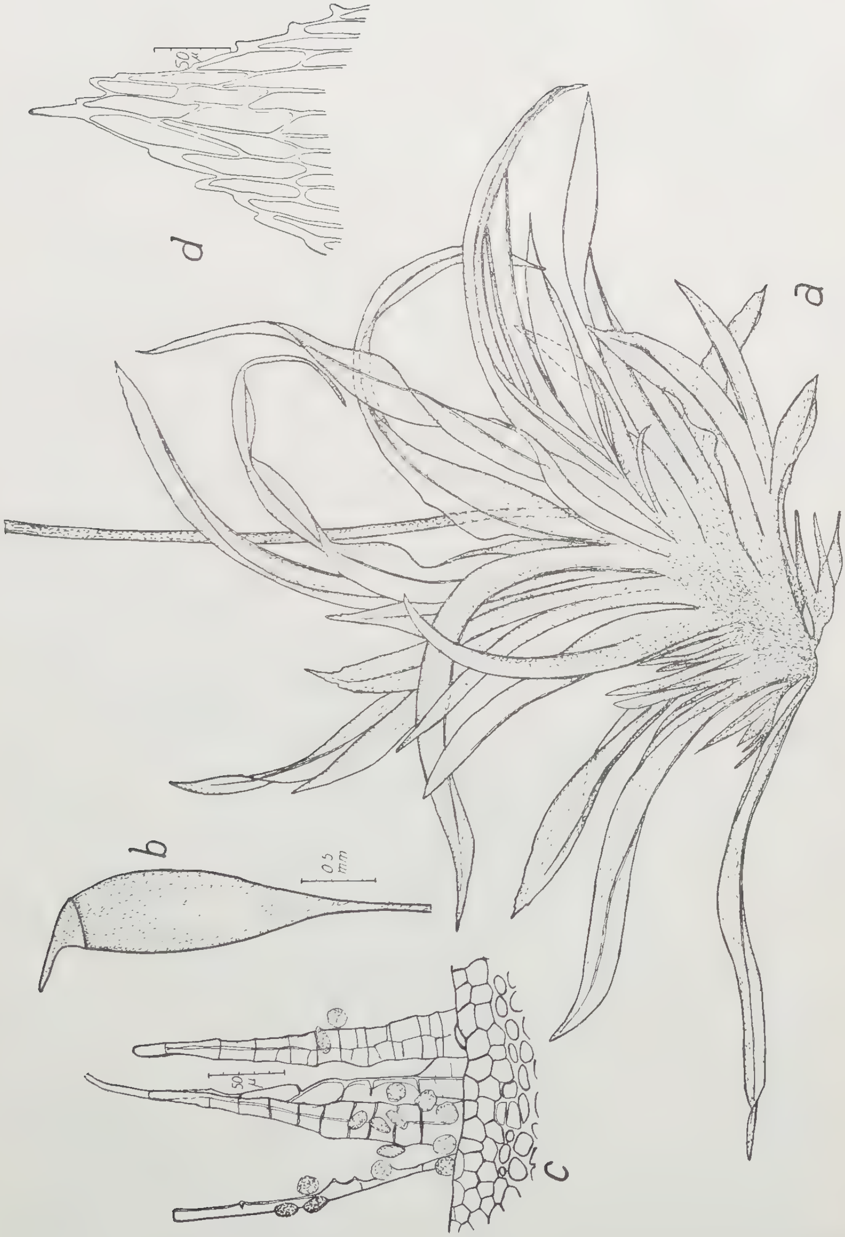


PLATE XV. *O. penticulatum*: *a.* Habit. *b.* Capsule. *c.* Peristome (isotype, L). *d.* Apex of leaf (isotype, L).

Differing from *O. pellucens*, in the somewhat more pointed leaves and the more robust peristome (Table II).

Seta generally longer (14 mm). (Plate XVI).

Examined specimens:

Colombia: Nova granata, sylvis Manzanos, 2700 m, leg. Lindig, no. 2111. (BM, type; NY; PC; U.S.; L; MEL).

Bolivia: Bergwald Rio Tacorani, 2600 m leg. Herzog no. 4054, 1911 (L, S, H, NY, PC); San Mateo-Sunehal, 2000 m, 1911, leg. Herzog, no. 4480 (L, S).

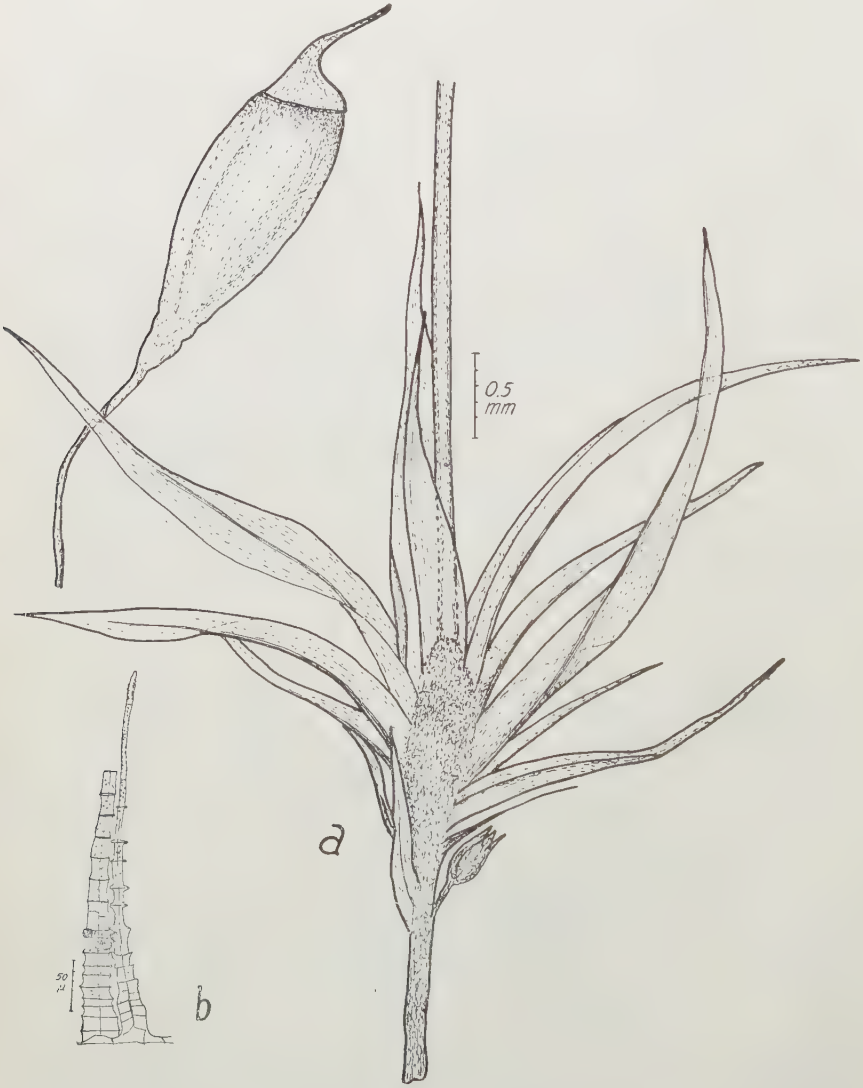


PLATE XVI

O. longisetum: *a.* Habit. *b.* Peristome (leg. Herzog, Bolivia no. 4054, L).

8d. **Orthodontium loreifolium** Besch. Fl. bryol. Reunion, 1880—1881; holotype in herb. PC.

Orthodontium brevifolium Broth. in Mildbread. Wiss. Erg. Deutsch Zentr. Afrika Exp. 1907—08, II: 153, 1914, with fig.; holotype in herb. H.

Orthodontium haplohymenium Dixon et Naveau. Naveau Musci Bequarti I, Bull. Soc. Royale Bot. Belg. LX: 35, 1928; holotype in herb. BM.

Description:

Generally a robust seta like *O. longisetum.*

Cell texture of the *pellucens* type, leaves at average longer and more pointed. Seta longer (10—20 mm). Maximal dimension of capsule somewhat larger (See Table II). Peristome pale, only the apex of the processes slightly papillose, in the examined specimens. (Plate XVII).

Discussion:

The delimitation of *O. denticulatum, O. longisetum, O. loreifolium, O. novae-guineae* and other related forms, which are described as separate species (*O. haplohymenium, O. brevifolium, O. emodi*), is rather difficult.

When we compare the different specimens we waver between the distinction of five or eight very slightly different species or the recognition of one species: *O. pellucens* sensu lato. When all local populations of this group were replacing each other geographically, we would be right in calling them all subspecies. But two of them are overlapping in South America with *O. pellucens*, namely *O. longisetum* and *O. denticulatum.* So they are probably no eco-geographical races of *O. pellucens.* There are no indications that they represent ecological subspecies. The only plausible hypothesis is, that they represent real species, isolated in their reproduction from *O. pellucens* sensu stricto. As the differences of the other more remote distributed forms are of the same degree as between *O. pellucens, O. denticulatum* and *O. longisetum,* the consequence of all these facts is in our opinion that they also cannot be lumped with *O. pellucens.*

Apparently they were isolated in the remote past from the main stock of *O. pellucens* and they developed gradually to special species, losing their geographical and genetical contact with *O. pellucens* sensu stricto. We have to do here in our opinion with one of the difficult cases of a transition between species and subspecies. The whole group can be called a superspecies in the sense of E. MAYR (1942), "Artenkreis" in the German language.

In the manner in which we have resolved the problem here there still exist rather big disjunctions in the ranges of several of the taxa. *O. loreifolium,* originally described from Réunion, is lumped here with *O. brevifolium* and *O. haplohymenium* from Central Africa (both possessing a double peristome). This is done because the morphological differences between these local forms are so slight that specimens of these forms could not be named without knowing their locality.

With the exception of matured small sporogonia we have to do here with comparatively robust capsules with rather long setae. It is sometimes not possible to distinguish the leaves from those of *O. pellucens* sensu stricto, but some individuals show a tendency to develop acuminate leaves, a character which is more pronounced in *O. novae-guineae* and *O. emodi*, nom. nud. We find the same character indicated at *O. longisetum*, a species differing however in its more robust, distinctly papillose and dark coloured peristome. *O. novae-guineae* is

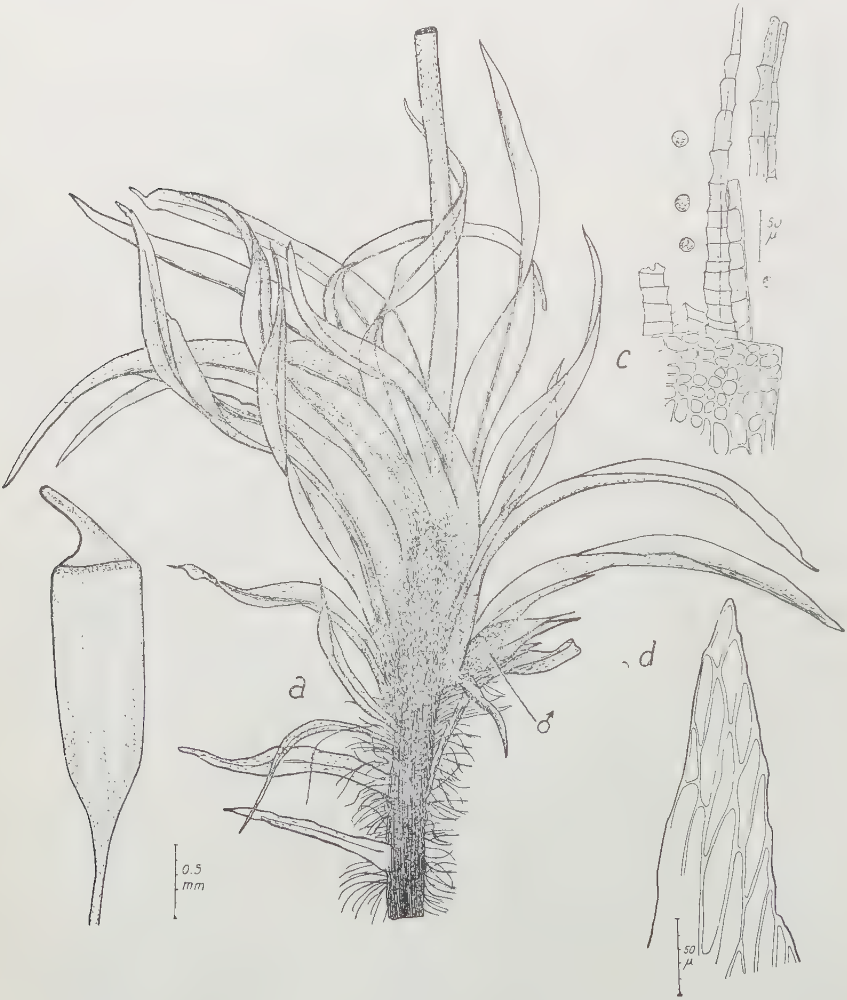


PLATE XVII

O. loreifolium:
a. Habit (type of *O. brevifolium* Broth, H).
b. Capsule (type material, PC).
c. Peristome (Réunion, Lepervauche, K).
d. Apex of leaf (type material, PC).

taken together with *O. emodi* on analogous grounds. This species represents a variation of *O. pellucens* with somewhat shorter setae than *O. longisetum* and *O. loreifolium*, a pale peristome, more like that of *O. denticulatum* and rather acute leaves, compared with *O. pellucens* sensu stricto.

TABLE II

Variation of some characters in the superspecies *Orthodontium pellucens*

Species	O. pellucens	O. denticulatum	O. longisetum	O. loreifolium	O. novae-guineae
seta-length in mm. . . .	5—17	7—14	14—16	9—20 (1,3)	7—15
capsule, length	1,30—1,85	1,6—1,8	1,8	1,65—2,2	1,2—1,8
capsule, breadth in mm .	0,50—0,65	0,60—0,80	0,60—0,65	0,60—1,00	0,50—0,60
length outer peristome in μ	200—290	160—220	320	185—320	180—240
length inner peristome in μ	150—300	160—225	370—400	250—300	250—290
diam. of spores in μ . .	15—20	15	15	15—20	15—20
length of the lid in mm	0,35—0,75	0,50	0,80	0,60—0,95	0,40—0,65
leaf apex bl. or acute . .	bl.	bl.	ac.	ac.	ac.
peristome papillose or smooth	pap.	sm.	pap.	sm.	sm. + pap.

Examined specimens:

Type collection:

La Reunion: G. de L'Isle, no. 209, 1875 (PC); other coll.: leg. Lepervauche, 1880, (K, herb. Bescherelle).

Type of *O. brevifolium* Broth:

E. Africa: Ruwenzori Butagn-Tal, Ericaceeen-wald, 3300 m, leg. Mildbread, 1908 (H); other coll.: Kilimandscharo, unterer Raganwald leg. A. Engler 2600 m, no. 1735, 1902 (H).

Type of *O. haplohymenium* Dixon et Naveau:

Central Africa: Ruwenzori Butagn. ca. 3000 m, leg. Bequaert, 1914 (PC, BM); other coll.: Mohanga, 3310 m, leg. Le Roy (Br); Ruwenzori, Uganda, Bujaka Valley near Bigocamp, 3300 m, leg. Olov Hedberg, 1948, no. 376 and 454 (herb. Uppsala & Potier de la Varde); Kenya, Aberdare Range, Kinangop, 3050 m, leg. O. Hedberg no. 1637, 1948, (herb. Uppsala, WM):

8e. **Orthodontium novae-guineae** Dixon. Papuan Mosses, Journ. of Bot. 1942.

Orthodontium emodi Hampe nom. nud., in herb. BM.

Description:

Growing in short tufts. Autoecious or heteroecious (the latter accordingly to Dixon lit. cit.).

Leaves glossy, yellowish green, length 2,3 –3,3 mm. Shape variable; one collection (Brass 12480) showing rather broad shortly acuminate leaves and some leaves blunt and toothed near apex, another collection (Brass no. 12334) possesses narrower leaves, more longly sharply acuminate, just like the type collection (Carr).

Vegetative parts much resembling *O. pellucens* and *O. loreifolium*, but somewhat smaller.

Seta 9—15 mm, capsules of very different dimensions (length 1,2—1,8 mm), longly ovate, regular plicate when ripe, lid 0,6—0,7mm, rostrate.

Peristome light yellow coloured or translucent, at maturity distinctly papillose, the inner as well as the outer. Inner peristome somewhat translucent and slightly narrower than the outer, outer peristome and processes rather long (till 290 μ). Spores 15—20 μ. (Plate II 3b, XVIII).

Discussion:

Very narrowly related is *O. emodi* Hampe nom. nud., from the Sikkim Himalaya. The collection of this form seems to me to be practically identical with *O. novae-guineae* and also very difficult to separate from *O. loreifolium.* It bears also glossy leaves, gradually pointed, it is autoecious, it bears gemmae (of 6—8 cells), the leaves are sometimes slightly dentate at apex. The capsules are regular ribbed when dry, their setae have approximately the same length (8—15 mm), the peristome is rather stout.

It is only preliminarily that *O. novae-guineae* is maintained here as a separate species and *O. emodi* nom. nud. as part of it. More collections from the Himalaya and Malaya mountains ought to reveal their real status.

The concepts which different bryologists have about *O. novae-guineae* differ extremely. DIXON stated after his type description (1942): "*O. infractum*, *O. sulcatum* and *O. australe* have shorter seta, less developed outer teeth and well-developed processes".

Comparison with the descriptions, given in this revision of the above named species, will show that real differences in seta length don't occur and that well-developed processes are a feature which these three species have in common with *O. novae-guineae.* BARTRAM determinated in his herbarium the collection of BRASS as *O. sulcatum* (Hook.) f. et Wils. In our opinion *O. sulcatum* is such a variable species that it should not be totally impossible to include *O. novae-guineae* in it. Some collections of *O. sulcatum* show fairly glossy leaves, a rostrate lid and a seta length of 11—14 mm, for example Weymouth's collections of Recherche bay, Tasmania.

In our opinion the resemblance between *O. novae-guineae* and some forms of *O. sulcatum* is only apparently. The differences in length of capsule lid, in the dimensions of the peristome and the toothing of the leaves are enough to consider it as more narrowly related to *O. loreifolium* and *O. pellucens.* The ripe peristome of *O. novae-guineae* is too much papillose, sporogonia and leaves show too great dimensions, to make it possible to put this species together with *O. infractum.*

It is not impossible that the existence of this New Guinean-Himalayan species indicate that *O. pellucens* as a superspecies (*O. pellucens*, *O. loreifolium* and *O. novae-guineae*) took his origin somewhere in the Australian region.

EXPLANATION OF PLATE XVIII

O. novae-guineae:
a. Habit (type, BM).
b. Capsule (isotype, L).
c. Peristome (type coll., BM).

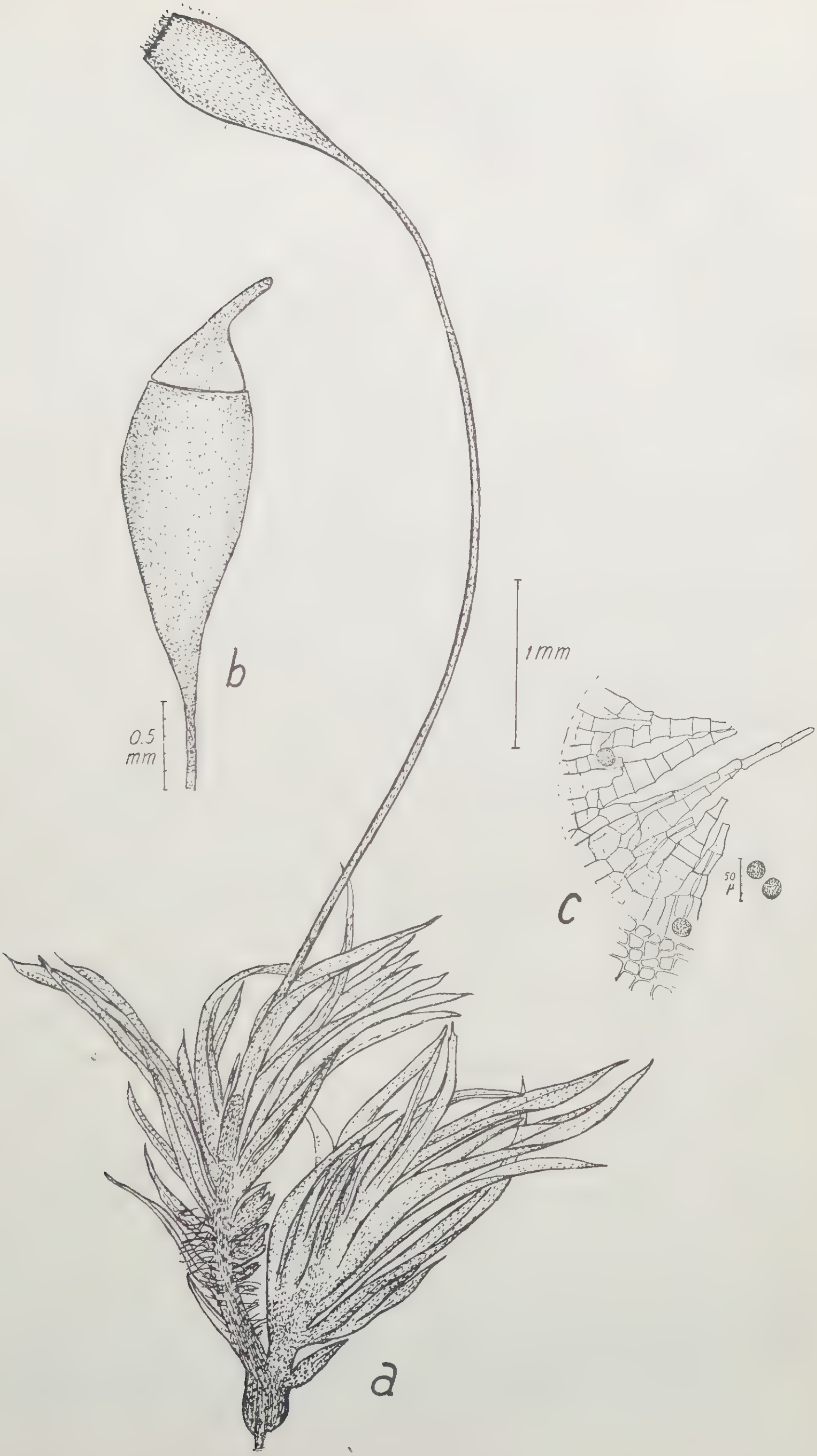


PLATE XVIII

N. Guinea. The Gap, Forest, 7200 ft, leg. Carr, 1936 (BM, type; L); Mossy forest, 18 km S.W. of Bernard Camp, Idenburg River, 2150 m, leg. L. J. Brass, no. 12480, 1939 (herb. Bartram); Mossy forest, 13 km S.W. of Bernard Camp, Idenburg River, 1800 m, leg. Brass no. 12334, 1948 (herb. Bartram).

Sikkim Himalaya, 7000 ft, J. Kurz. 2934 (BM, type *O. emodi* Hampe, nom. nud.; NY).

Species dubiae et excludendae.

Stableria(?) ruwensorense Thér. et Naveau.

Naveau, Musci Bequarti: Bull. de la Soc. Royale de Bot. de Belgique. Tome LX (Diexième Serie, Tome X), fasc. I, 1927, p. 34. Sterile specimen in herb. Br. Certainly no representative of section Stableria or any species of section Orthodontium.

Orthodontium itacolumitis C.M. Bull. Herb. Boissier, 1898, p. 30; in herb. PC and H. The type material is for me too scanty and it bears too young sporogonia to settle the position of this form.

6. SUMMARY

The chief results of the taxonomic study of the genus Orthodontium are the following.

A close study of the different characters used in the taxonomy of the genus reveals that many of them are to a certain extent so variable that they cannot be used without reserve for the delimitation of taxa, namely dimension of the sporogonia, relative length of the teeth of inner and outer peristomes, papillosity or smoothness of peristome and sulcation of the capsules.

The consequence of this is that BROTHERUS' sections (1909), which were chiefly based on these characters, must be considered as artificial. A more natural arrangement of the genus is achieved after recognizing the slight variability of the following characters: length of the lids, reduction of inner peristome, the lack or possession of collenchymatous cell walls near the margin of the capsules, the distribution of the sexes (to a certain extent), the cross section of the leaf nerves, and even the glossiness of the leaves.

The following characters can probably be modified by mutations: the length of setae, the breadth of the leaves, the papillosity and the dimensions of the peristome, the size of the spores and the toothing of the leaves. But these characters also vary according to the habitat. We must thus be very careful in using them in our taxonomical considerations.

After revealing more of the real affinities between the species, a better subdivision of the genus could be tried. All the described species of the genus Stableria are to be considered as representatives of one species which possesses in different climates and habitats somewhat different modifications. This species, *Orthodontium gracile* Schwaegr. ex Br. et Schimper, possesses so many characters in common with other species of Orthodontium, for example the cell texture of the leaves and the type of the peristome (key characters for the whole genus, within the family Bryaceae), that it can be only a member of a separate section, the section Stableria (Lindb.) W. M. This section is different from the other section (Sect. Orthodontium) in the type of the nerve, and in some details of the structure of the sporogonia.

Within the section Orthodontium there can be distinguished two groups of species, though there cannot be drawn a sharp line of demarcation between these groups. They can be arranged around two highly polymorphous species: *O. pellucens* (subsect. Pellucens) and *O. lineare* (subsect. Linearis).

A further consequence of the morphological study of the genus is that many species names are considered to be superfluous. Of 33 names, 12 remain as names of species or subspecies and among the more recent collections two new taxa have been described. It has been pointed out that *O. pellucens* s.l. must be considered as a superspecies, a species which is represented in tropical America, Africa and Asia by different closely related forms (*O. pellucens* s.s., *O. loreifolium, O. novae-guineae*). The type of species formation within the subsection Pellucens in South America, reveals that the most adequate treatment of this complex is a treatment as a superspecies (Artenkreis). The members of the subsection Linearis are the most variable and accordingly the most difficult. Totally satisfactorily results could not yet be reached here. It is not impossible that hybridization played a role. Nevertheless, in this subsection several species names are to be considered superfluous, after careful study.

An interesting result of this study is that there exists no sharp line of demarcation between the South African *O. lineare* Schwaegr. and the Australian *O. sulcatum* Hook. fil. et Wilson.

They differ chiefly in their range of variation. That's why they are both considered as subspecies of *O. lineare* Schwaegr.

The problems in European bryology, about the real status of *O. gracile* var. *heterocarpum* Watson and *O. gaumei* Allorge et Thériot, are resolved in the following way.

The first must be considered as a part of *O. lineare* Schwaegr. and of the second it is very probably that it belongs to *O. pellucens* (Hook.) Br. eur.

In this way the picture of the taxonomy of this genus is totally changed. Several taxa appear to have a much greater range than has been supposed in former days.

CHAPTER IV

ORTHODONTIUM LINEARE IN EUROPE

In the year 1927 the British bryologist W. WATSON distributed under the name *Orthodontium gracile* Schwaegr. a specimen of Orthodontium, collected by him and by H. C. BROOME on gritstone rocks, which were surrounded by peat, near Crowden (Cheshire).

We read the following about this find in the Moss Exchange Club Report:

"A remarkable form, perhaps a distinct species, and certainly a good variety. From all my samples it differs in being more rigid, in its sub-falcate, secund leaves, which are less flexuose and shorter and have mostly much shorter and broader points; and in its shorter, broader, often sub-pyriform capsule, which in age is sometimes markedly asymmetrical. The processes of the endostome show under a high power minute punctate markings, which I could not see in any of my ordinary gatherings with which I compared it, and there are other differences in the processes. The spores are as in the typical plant. It could be passed in the field very easily as a *Dicranella*".

In the next year W. WATSON published this new discovery as variety *heterocarpa* (more correctly spelt *heterocarpum*) of *Orthodontium gracile* Schwaegr. ex. Br. & Schimp. (WATSON 1922). He gave the following description of this variety:

"Differs from the type in the shorter broader often more or less gibbous capsule, which may be smooth or deeply sulcate, straight or curved (sometimes very strongly so). Teeth of inner peristome minutely punctate. Antheridia usually in separate gemmiform groups".

Of course this new find came also under notice of H. N. DIXON, in those days the leading man of British bryology. He made the following notitions on the herbarium sheet of the Crowden collections:

"Autoecious, paroecious and perhaps dioecious. D. A. JONES in litt. On this account and the rather large turgid somewhat gibbous short necked capsule it seems well worth a var. name.
H.N.D. 3.21.

Later described as var. *heterocarpa* Watson. I am almost inclined to think it specifically distinct — I cannot separate it from *O. lineare* Schwaegr.
H.N.D."

These notes, now in herb. Kew, were somewhat amended in DIXON's Handbook (1924) where we read: "Recent investigations indicate that it may prove to be a distinct species".

Certainly DIXON had in mind then the work of W. H. BURRELL, who had this peculiar moss in close observation. We learn that from his letter of July 23d 1923 to Dixon, kept in the Kew herbarium. This letter is such a vivid report on the first dissemination of the so called var. *heterocarpum* in England, that I'll cite it here.

> "Will you kindly tell me what value should be placed on BROTHERUS' treatment of Orthodontium in ENGLER? If striation of capsule, texture of inner peristome, state of inflorescence and habitat, taken collectively, are of specific value, there should be two plants in Yorkshire as suggested in WATSON's paper J. of Bot. 1922. At any rate I may tell you my experience with the plant, with the hope that it may ultimately lead to another of your nice little reviews of a genus from a worldwide standpoint. At Bolton Abbey (Strid) and at Plumpton by Knaresborough it

grows on perpendicular faces of massive gritstone rocks, and is so limited in its distribution that the rock at Bolton where I know it, is probably the spot where SPRUCE knew it, and it appeared to be restricted to a similar small place at Plumpton.

Le J. COCKS gathered it at Birk Crag Harrowgate in 1912, a millstone grit area; he would probably have specially noted the fact had it not been on a rock.

The gatherings from these three stations in my herbarium were gathered during the winterhalf of the year, Sept. to March and are not in good condition, but the slides enclosed show they are paroecious as fig. 405 D. ENGLER, and the old capsules present are smooth.

Gatherings made during the past 18 months near Huddersfield, Ingleton and Penistone were growing on peat (partly on Birch boles at Raikes Dyke); the capsules are striated and the male inflorescence gemmiform, autoecious. All the antheridia are axillary in the rock plant and I have no definite evidence that any are axillary in the peat plants.

The statement in WATSON's paper that the inflorescence is variable has not been overlooked, but in the only case of that kind that came under notice I suspected two seasons growths were involved, young male organs showing above old archegonia; this however needs further elucidation.

Recently the Y.N.U. held a weekend meeting at Penistone; on the Friday evening, during an after supperstroll, Orthodontium turned up within 2 miles of the town, on a small piece of moorland, associated with *Calluna*, *Vaccinium* and *Aira flexuosa*, on peat.

Saturday was spent in the Little Don Valley above Langsell Reservoir; the plant turned up early and was seen repeatedly during the day. On Sunday Midhope Moor was visited and again Orthodontium was the outstanding moss from the start about 750 ft. to the deep peat bogs at 1600 ft. under Cloudberry.

In one place the side of a peat pool had an area of 3 sq.ft. covered with capsules like that enclosed in the box. I saw none on rock; although there was a good deal of variation in the capsule, both in apparant texture, shape and sulcation, this appeared to be at least partly due to state of development; where striation was hardly evident, the microscope shows traces. I do not understand how the plant in such profusion can have been overlooked. Is it possibly a new comer, now in the rampant stage, like *Matricaria suaveolens*?

The points that impress me are:

the habitat
the inflorescence
the striated capsule
the papillose processes (about 0.15 mm long)"

The most striking item in this letter is the passage: "Is it possibly a new comer . . . .?"

Seventeen years later BURRELL devoted a special extensive paper to the whole problem (BURRELL 1940). He stated that all gatherings of Orthodontium before 1900 in England belong to WILSON's *Bryum gracile* (= *O. gracile* Schwaegr. ex Br. et Schimp.). The earliest known gathering of the so called variety *heterocarpum* Watson is made by E. A. RICHARDS, from Overton Hills, Cheshire, May 1911, according to BURRELL's examination of the most important British collections. BURRELL (1940) gave a map showing that till 1940 the variety had spread over an area of approximately 160 miles in length in the central parts of England, centered round Cheshire and Yorkshire.

Of course several questions arose around the so called variety *heterocarpum*. Was it a real variety of *O. gracile*, or was it a separate species? What was its origin?

All the known facts indicate that it had only recently been on the moors. Two possibilities exist for its origin there, either it arose by introduction, or by mutation from *O. gracile* Schwaegr.

The last named species is rather frequent in the same area where the variety had been found first, but it occurs also farther away, in Sussex, Devon and Southern Scotland (map in BURRELL 1940).

While BURRELL only touched the first possibility in his letter to DIXON (deposed in Dixon's herbarium, Kew) he gave in his publication of 1940 preference to the second hypothesis. His conclusion was:

"WATSON's variety *heterocarpum* appears to be a true breeding, very fertile, fixed mutation, that has established itself in Cheshire and the adjacent countries, during the past fifty years, and is still spreading".

Now it is true that var. *heterocarpum* is more robust, more hardish, and more fertile than *O. gracile* Schwaegr., at least in England. While *O. gracile* Schwaegr. has a very constant area, the so called variety is still spreading. Nowadays it has already reached Eire and Scotland. But we shall see that all these facts are no proof that it is a mutation, as BURRELL suggested, or to be more specific a polyploid form of *O. gracile*. We should investigate as well the other possibility, and perhaps with a better result, namely introduction of the var. into England. The last supposition is for example more probable, because the differences with *O. gracile* are quite on the scale of species differences in the genus Orthodontium. We have seen that they can even be treated as differences between two sections of the whole genus.

So BURRELL's hypothesis means no less than a macromutation, performing itself under our eyes. Perhaps the few lines which BURRELL devoted to the possibility of introduction into England offer the real solution of the problem. We read on page 298 of his paper: "TRAVIS reported the introduction of mosses to the Mersey with timber; Orthodontium grows on living and dead wood as well as on peat and rock, but there is no evidence in support of alien immigration."

New investigations on this problem started after the spreading of the so called var. *heterocarpum* to the continent. It was collected by the author on an excursion with his friend W. VERGOUW in the nature-reserve Naardermeer, Holland, on the 22nd of March 1943.

Sporogonia were in such a young state that the sample could be named only after some difficulty (MEIJER 1948, MARGADANT and MEIJER in AGSTERIBBE c.s. 1950).

Starting from this find, MARGADANT and MEIJER (1950) published a study of all known species of Orthodontium in Europe, in which they stated that this so called variety had to be named identical with *O. lineare* Schwaegr. and that *O. germanicum* F. & K. Koppe belongs to the same species. REIMERS (1941) had previously stated that the var. is identical with *O. germanicum.*

We did not know anything about DIXON's suggestion that he could see no difference with *O. lineare.* Apparently nobody noticed that. In a preliminary study of the whole genus it seemed probable that the variety had nothing to do with *O. gracile.* It became gradually apparent that its distribution over Western Europe was amazing and the insight grew that it could be an immigrant, introduced by human influence (MEIJER 1951). It was a pity however that attempts to establish the chromosomenumbers of both forms had no success in England and no more in Holland, because the plants are very difficult objects for cytological studies. Polyploidy is not very evident however on theoretical grounds, though it should not be excluded in our minds. It is not likely that we should get by autopolyploidy from *O. gracile* a species that is autoecious or heteroecious instead of paroecious, and which has quite another structure of peristome, papillose instead of smooth, with broad processes instead of narrow, with a band of collenchymatous cells near the mouth on the capsule instead of parenchymatous and with approximately the same size of the spores and the same cell dimensions.

Analogous to the result of WETTSTEIN (1932) we could only await plants with greater cells, more robust habit and with reduced fertility, at least in the first generations.

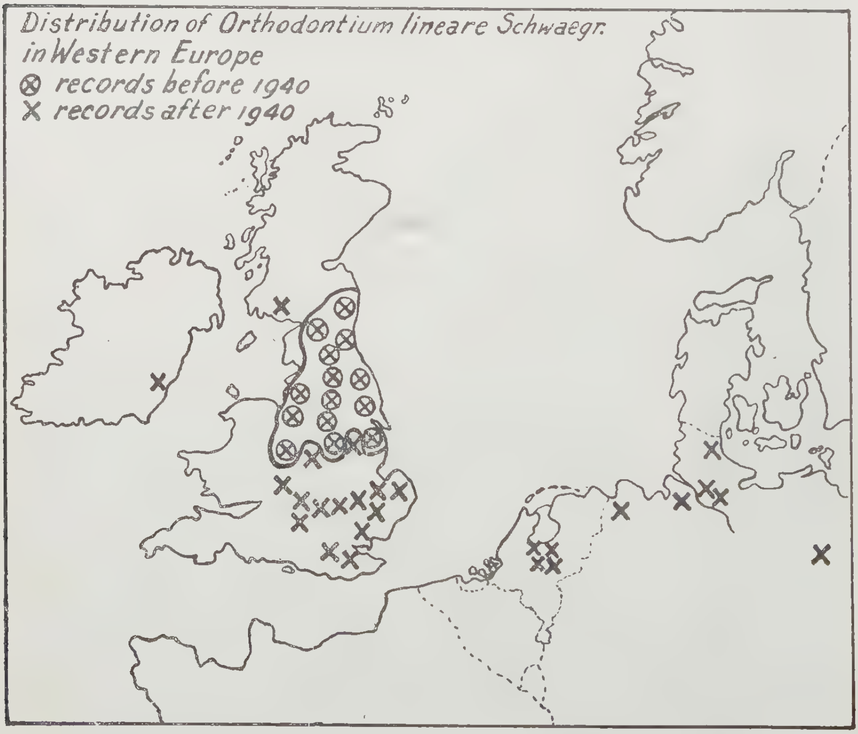
What evidence exists in support of alien immigration of *O. lineare* into England? TRAVIS reported the introduction of mosses with timber along the Mersey. Now this is the river near Liverpool. It is here that Orthodontium could be introduced from the Cape Colony. The place where it first had been collected is just south of Liverpool in Cheshire and another locality is situated 50 miles (80 km) to the N. East. Afterwards the spores must have been carried 300 km and more, before they found suitable habitats in Holland. The study of plants from England, Holland and Germany revealed such a great mutual resemblance that it is in our opinion not impossible to assume that they all are derivatives of one tuft.

Mr. W. G. TRAVIS was so kind to give us the following valuable information about imports of timber with mosses near Liverpool.

> "The sentence in BURRELL's paper in the Naturalist (1940) which you quote, is evidently based on the fact that in 1920 and some subsequent years I sent some moss specimens to the Moss Exchange Club, collected from the bark of timber imported into Liverpool.

In the years 1920—1924, my brother, who was in a firm of hardwood timber merchants in Liverpool, used occasionally to give me tufts of mosses and hepatics, which he scraped off the bark of tree trunks imported by the firm from abroad. These included, at different times, samples of mossgrowths that he happened to notice on the bark of logs or trunks, e.g. from the Caucasus region, Asia minor, on boxwood (*Buxus sempervirens*); Kamerun (West-Africa); Cape Colony (South Africa), and from the U.S.A.

It is about the specimens from South Africa that will be of interest to you. The mosses were named for me by Mr. H. N. Dixon; and I contributed some packets of specimens to the Moss Exchange Club. The timber came from Cape Colony, Knysna and East London, or was shipped from those ports. The mosses were all barkgrowing plants. There was no *Orthodontium lineare* among them, ..."


Distribution of Orthodontium lineare Schwaegr. in Western Europe
⊗ records before 1940
X records after 1940

MAP 1

So far Mr. Travis.

It is of course not impossible that Orthodontium was at least once among the mosses imported in this way. We should stress the fact in this connection that Knysna is laying only some 80 km from George where *O. lineare* has been collected by Pillans in a form which is almost identical with the European. Sub-tropical rainwoods are or were found there.

About the stations near Liverpool Mr. TRAVIS wrote me:

> "The Crowden locality of Watson is about 10 miles S.E. of Oldham and is in Yorkshire. This locality is fully 40 miles distant from Liverpool. The nearest station to Liverpool that I know of *O. lineare* is on peaty heathy ground at Thurstoston Hill, about 6 miles S.W. of Birkenhead, Cheshire, (bank of the Mersey, opposite to Liverpool, W.M.), where it was discovered a few years ago (about 1944 or 1945), long after the date of WATSON's paper (1922). It may of course have been long present in that station, but passed over by local bryologists as *Dicranella heteromalla*."

In our opinion we are now not far from the truth when we state that all known facts justify the conclusion that *Orthodontium lineare* is an immigrant in Europe, just like *Elodea canadensis*, *Vaccinium macrocarpon*, *Aronia melanocarpa*, etc.

It is quite understandable that not all samples from S. Africa are to the same extent identical with the european. Only one tuft out of a variable population could be the ancestor of the more uniform European populations. (Map 1).

Map 1 gives an impression of the present known distribution of *O. lineare* in Europe, compared with its known range up till 1940.

We thank the new dates of the distribution in England to Mr. E. F. WARBURG, the recorder of the British Bryological Society and from Germany we got them from Dr F. KOPPE (Bielefeld). In Germany till May 1951 twelve stations were known.

CHAPTER V

GEOGRAPHICAL CONSIDERATIONS

1. DISTRIBUTION OF THE TAXA OVER THE WORLD

The distribution of the genus Orthodontium over the world is rather discontinuous. The greatest range possesses *Orthodontium gracile:* California, Central and South America, Central Africa and Abyssinia, N.W. Europe (Map 2).

O. pellucens has numerous stations in South and Central America. Moreover it occurs on some islands in the Caribbian Sea[1], in California, Tennessee, Galapagos Islands and Hawai. In South America it is not restricted to the Western part as is *O. gracile* (Map 3).

The closely related species *O. loreifolium* is scattered over Africa and Asia: Réunion, Ruwenzori, Kilimandscharo and Mt. Kenya.

Sikkim Himalaya and New Guinea are the ranges of *O. novae-*

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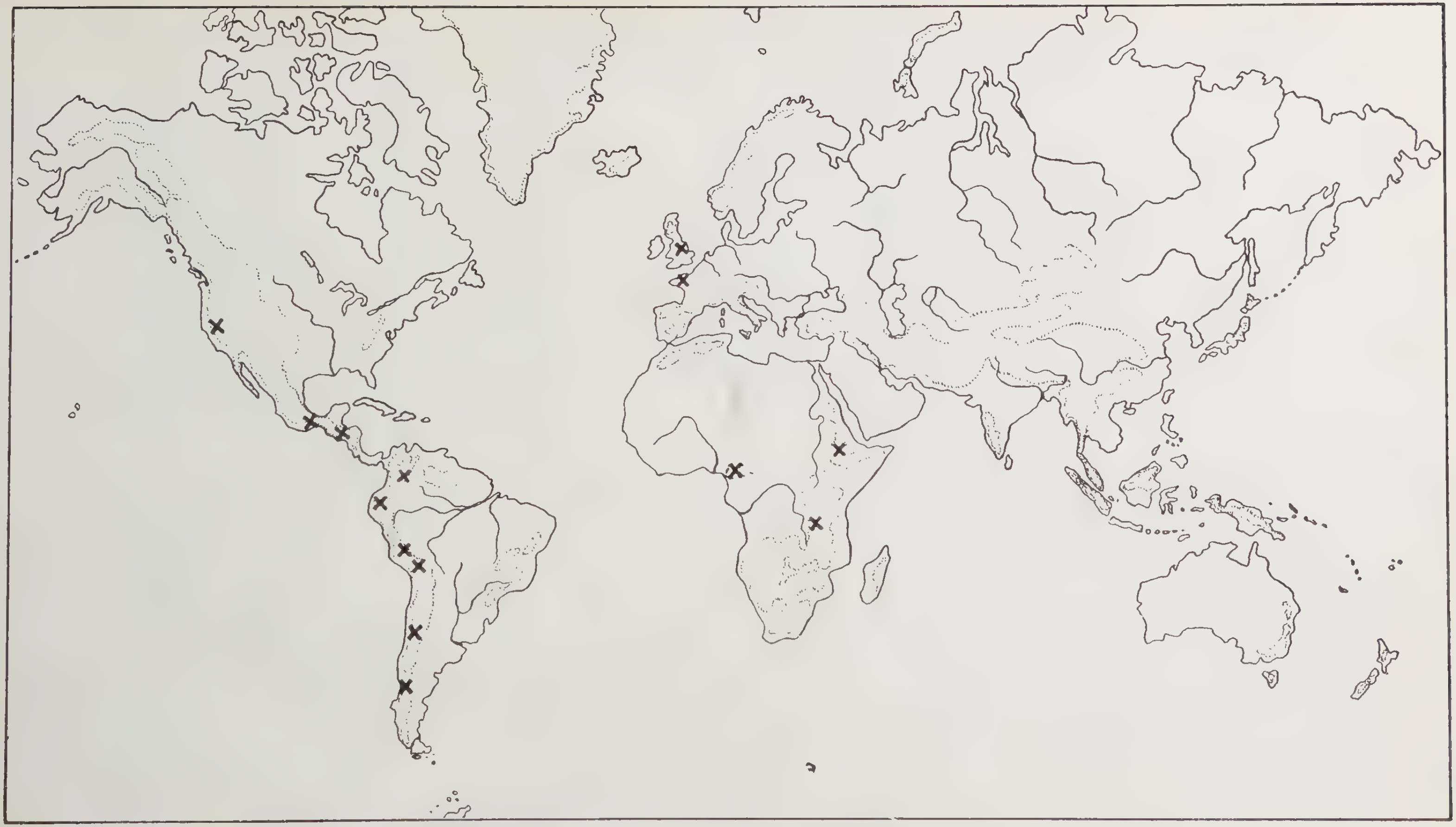
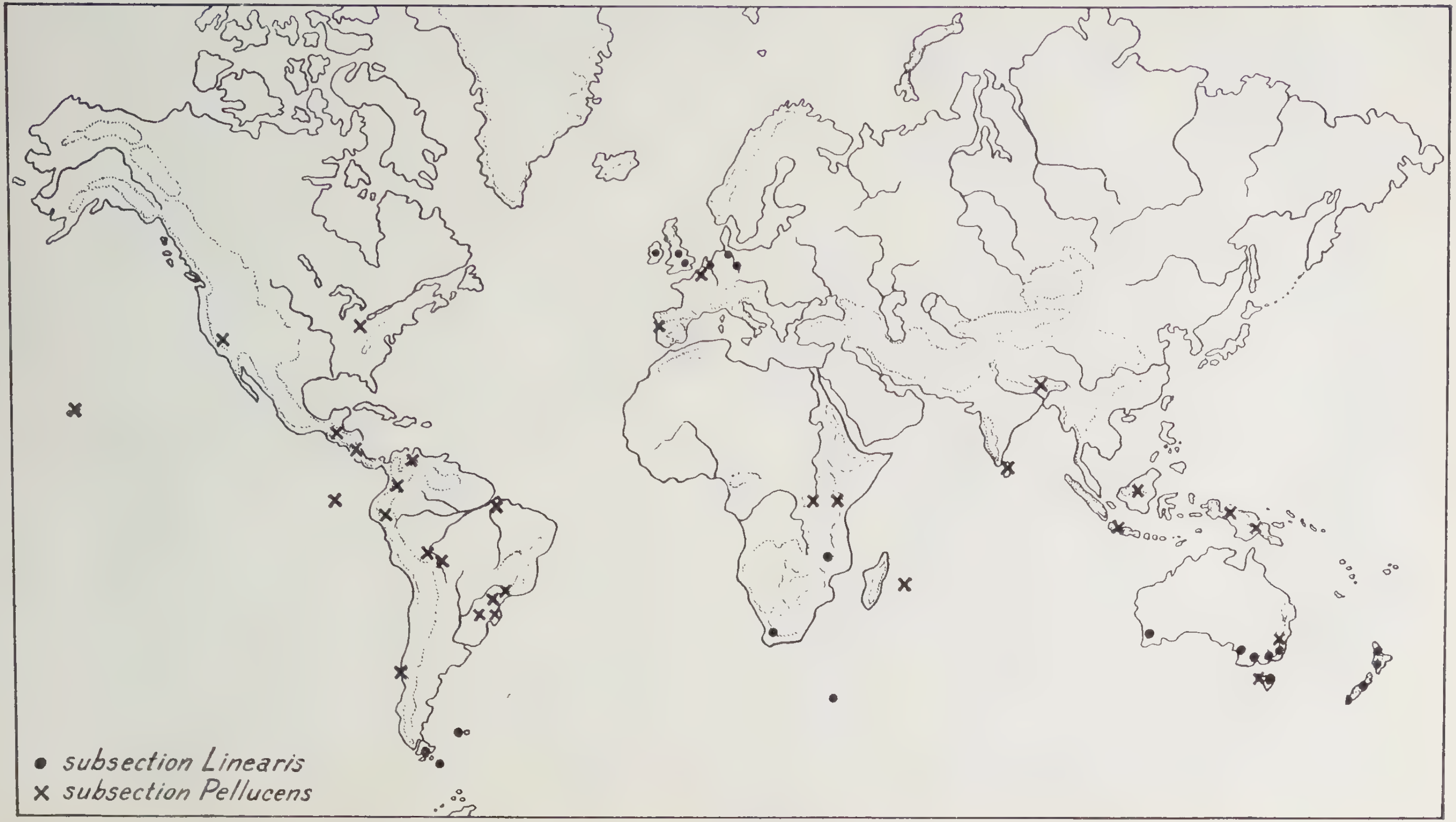
[1] Omitted on Map 3.



MAP 2 Distribution of *Orthodontium gracile* Schwaegr. ex Br. Schimp. over the world

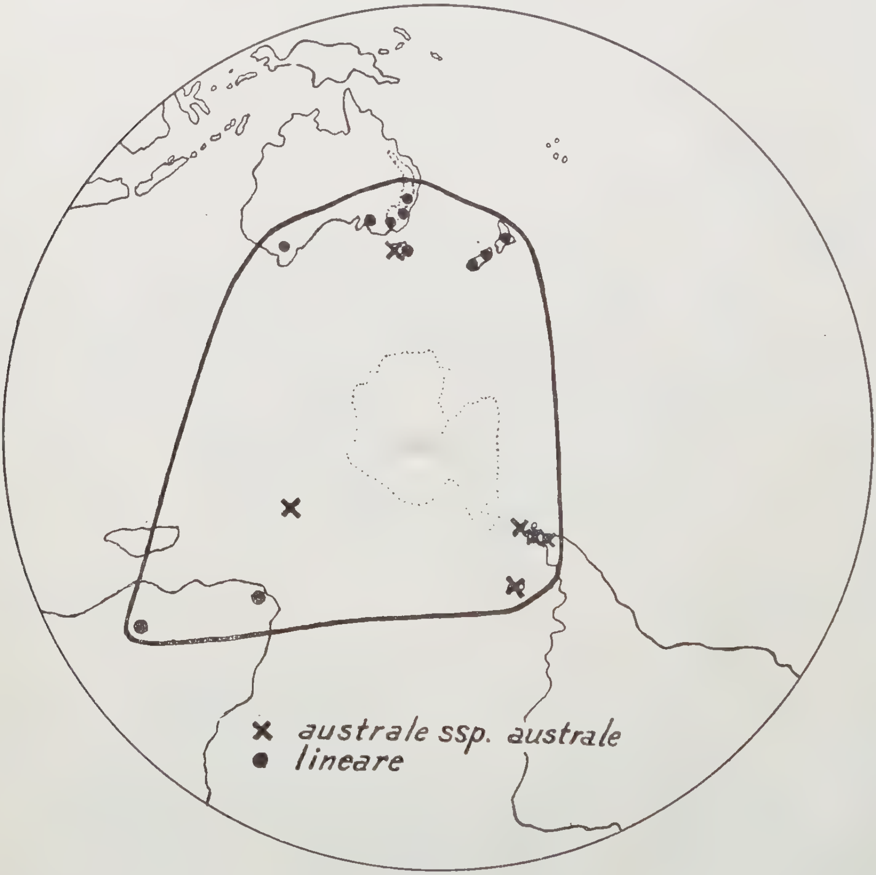


MAP 3 Distribution of Orthodontium Section Orthodontium over the world.

guineae. O. infractum is restricted to Ceylon, Borneo and Java. The related *O. inflatum* occurs in South East Australia.

The last region together with South West Australia, Tasmania and New Zealand forms the range of *O. sulcatum*. This species is closely related to the South African *O. lineare*, which possesses an outpost in Nyasaland.

O. australe, the most southern species, is restricted to Fuegia, Falkland Islands, Hermite Island, Marion Island and Tasmania (Map 4).



MAP 4
Distribution of *O. australe* ssp *australe* and *O. lineare* on the Southern hemisphere.

It is evident that the genus occurs chiefly on the southern hemisphere. Thereby it is interesting to note that the subsections *Pellucens* and *Linearis* are partly overlapping, *Linearis* being confined to more southern latitudes than *Pellucens*.

The relative frequency of taxa in certain regions of the world appears from the following table.

TABLE I

The number of species and subspecies of Orthodontium in different regions of the world

	Austr.	N. Am.	S. Am.	Africa	N.W. Europe	S.E. Asia
whole genus	6	2	4	4	2(3)	2
section Orthodontium (section Stableria excluded)	6	1	3	3	1(2)	1

We have to take into consideration that one species, occurring in N.W. Europe, is probably a rather recent immigrant, brought there by human influence (chapter IV).

It appears from the above table that the Australian region, including Tasmania and New Zealand, is the richest for Orthodontium. This is strenghtened by the fact that also the frequency of localities of the separate species according to the collections made, appears to be greatest there. When we compare the frequency of characters in these separate regions we get the following picture:

TABLE 2

Frequency of some differential characters in different parts of the world

	Austr.	N. Am.	S. Am.	Africa	N.W. Europe	S.E. Asia
pyriform capsule	×			×		×
paroecious infl.	×	(×)	(×)	(×)	(×)	
leaves without stereid cells		(×)	(×)	(×)	(×)	
inner peristome rudimentary	×					
extremely long setae (20 mm)	×		×			
distinctly dentate leaves			×			×
conical lid	×	(×)	(×)	×	×	
long beaked lid	×	×	×	×	×	×
Total	6	4	6	5	4	3
Orthodontium gracile excluded	6	1	3	3	2	3

The figures are not very high. We cannot conclude from them that Australia should be the centre of variation of the whole genus.

When we exclude *O. gracile*, which is by some authors considered as a separate genus (Stableria), we get another sum total of differential characters. For this reason, characters represented in a certain region only by *O. gracile* are put between brackets. From this it appears that within the section Orthodontium, Australia is not only the region with the greatest number of different species, but also the richest in characters. The different characters are rather widely distributed over the whole range of the genus. Perhaps this phenomenon indicates a rather high age of the genus. In this connection it is a remarkable fact that the Australian-Asian region is not reached by the section Stableria and that the subsection Linearis is lacking in Asia.

2. Habitat preferences

When we compare all the ecological notes, brought together from the stations were species have been collected, we discover that the whole genus is rather homogeneous in its habitat adaptations.

All species of Orthodontium favour moist habitats. They cannot stand long dessiccations, though a rather dry season is not unfavourable for *O. lineare*, during the fruitingstage. As far as we know all species are growing on acid substrates: peat, poor soil, dead tree stumps, sandstone rocks, etc. The ecological specialisation of the species does not show great differences. In tropical regions they only occur in the higher zones of mountains, in forests or in shrubs near the tree limit. Orthodontium avoids all dry tropical and continental regions of the world.

Now it is a well known fact that the general climate of oceanic regions in the temperate zones has much in common with the local climate on mountains in the tropics. Both are wet climates with a rather small amplitude of temperature during the year. Epiphytes, among them mosses, grow luxuriant in such climates. The life forms of plants of tropical mountains and of the oceanic islands on the southern hemisphere have many features in common (Troll 1948), a natural consequence of the similarity of the climate.

When we study, from the ecological point of view, the regions where species of Orthodontium are growing, we discover that all taxa are adapted to this mountainous or oceanic climate. This preference is partly the reason for the fact that the genus is chiefly distributed over the southern hemisphere and over the antarctic regions, where these climates are predominant.

We find species of our genus on the Andes of South America, through the Cordilleras of Middle America, on the islands in the Caribbean Sea, but always in damp mossy forests in wet mountainous climates. The same is true of the Central African Highlands, where it has been collected in the ericaceous shrubs and the vegetations with giant Senecio's, of Ruwenzori, Kilimandscharo, Mt. Kenya and the Highlands of Abyssinia. In the southern part of Africa Orthodontium is found in sub-tropical and wet temperature forests. In Australia the range comprises the mountainous parts of the southern temperate zone (S. of Queensland): the Australian Alps and the Blue Mountains. In Tasmania and New Zealand damp mountain forests as well as lowland stations are the localities of Orthodontium. In southern Chile, on Fuegia, Falkland Islands and Marion Island the sealevel is reached, just as in the atlantic parts of Europe and the redwood areas of California.

In the Asian region only the mossy forests on the vulcanos of Java, the mountains of New Guinea and the Sikkim Himalaya are the localities hitherto known. (Map 3).

These facts are sufficient to illustrate the preference of the whole genus for oceanic or temperate mountain climates.

From the foregoing paragraphs it will be clear that two special aspects play a role in the history of the genus:

1. the migration from some centre of dispersion.
2. the preference for oceanic mountainous climates.

It is very difficult to reveal the general trends in migration and evolution of the genus, in connection with the distribution of the different species and with their affinities. We might suppose that the distribution of the genus over the world has been determined by its ecological preferences only, assuming that the spores could spread all over the world. In this case the present areas would give information only about the ecological preferences, without any further data in connection with historic biogeography.

This assumption can be checked from two sides:

1. by direct knowledge of the probability or improbability of random distribution by wind drift of spores.
2. by a careful study of the types of the areas.

We consider the distribution of the species within those parts of the world, of which we may assume that they form the potential area of the genus: all oceanic and wet mountainous regions together. Then we discover that within this area not all the species are distributed in the same way. We can distinguish different types of distribution:

a. The *gracile*-type
Area comprising America, Europe and Africa. *O. gracile*, *O. pellucens*.
b. The *lineare*-type
Area comprising S. Africa and Australia. *O. lineare*.
c. The *australe*-type
Area comprising S. America, Marion and Tasmania. *O. australe*.

The other species-areas are of a more endemic type. The above named types of distribution (*a*, *b*, and *c*) relate to species which belong probably to the oldest in the genus, because they are highly polymorphous, while *b* and *c* may be considered from a taxonomic point of view as the centra around which the other species can be grouped.

These different types of area and the probability that the age of the area plays a role in their extent, are in accordance with the hypothesis that the distribution of species of Orthodontium is not merely a case of random spread of spores all over the world. It must be a distribution along certain lines of migration which is strongly influenced by the geographical history of the globe.

Why should *Orthodontium gracile* be missing in Asia and Australia when it could be easily distributed everywhere by its spores? Why should *O. lineare* be lacking in South America? The evidence for the above stated hypothesis becomes even stronger when we take into account that the same distribution types *a*, *b*, and *c* occur among phanerogams (IRMSCHER 1923, CAIN 1944, WULFF 1943).

3. ANALOGOUS DISTRIBUTION PATTERNS IN OTHER GROUPS OF PLANTS

a. *O. gracile*-type.
There are many taxa of musci which are restricted to America and Europe-Africa, namely two families, 36 genera, 8 subgenera and sections, 144 species, totalling 190. In phanerogams there are relatively more genera, but less species of this type of distribution.

b. *O. lineare*-type (S. Africa-Australia).
This disjunction is paralleled by some mosses like *Gigaspermum repens*, *Campylopus bicolor* and *Pleuridium nervosum*. Among phanerogams this is paralleled by two genera of the Restionaceae: *Restio* and *Hypolaena*.

c. *O. australe*-type (S. America, Marion, Tasmania).
IRMSCHER (1923) gives examples of several other taxa (genera and species) with analogous distribution in the southern hemisphere, in total 1 family, 8 genera, 3 sections and 18 species. Among mosses and hepatics this is a rather common type of distribution. Parallel cases among phanerogams are the genera *Acaena* (Rosaceae) and *Weinmannia* (Cunoniaceae). They belong to the so called *Azorella*-type. Examples among mosses are *Ptychomnium mülleriella* and *Blindia magellanica*.

In this way we can understand that HERZOG (1925, 1926) as well as IRMSCHER (1923) and WULFF (1943) make use of distribution areas of special taxa of mosses as additional support for the theory of continental drift.

But without exact direct knowledge of the effect of spread by spores, all our considerations remain very speculative.

We must admit that we know very little about this topic.

An illustrative example is the discussion of PERSSON (1944) with PETTERSON (1940), about the occurrence of spores of the mosses *Aloina brevirostris* (Hook. & Grev.) Kindb. and *A. rigida* (Hedw.) Dixon, in rainwater in Finland. Both species are lacking in Finland. PETTERSON accepted the hypothesis that these spores came from Siberia, but PERSSON made evident that they might originate from stations nearer by.

Fortunately we have some exact direct indications now of the spread of *O. lineare* from England to the continent. At least some hundreds of kilometers between the Middle-England stations and suitable places on the diluvial parts of Holland have been bridged by the spores. Within a few decennia this species has spread from Middle England to Schleswig-Holstein, at the Danish-German border.

Such a spread is more rapid than in the cases of phanerogams as e.g. *Anthoxanthum aristatum* and *Galinsoga parviflora* in Holland.

On the other hand, when we take the genus Orthodontium as a whole, it is likely that the wide and disjunct distribution of several of its species cannot be accounted for, without assuming a formerly, more extended, antarctic continent, though it is not inevitably necessary to assume simultaneous landconnections between the exact recent areas in S. America, Tasmania and New Zealand.

4. Conclusion

From the foregoing considerations we draw the following conclusions:

1. The genus Orthodontium is especially distributed in temperate oceanic and tropical mountainous climates, consequently the chief part of its area is situated on the southern hemisphere.
2. Distribution of species within this area cannot be a result of unlimited airborne spread of spores, but it is certainly influenced by the distribution of seas and continents in former ages.
3. Spread by means of spores is possible within a favourable climate, at least over distances of some hundreds of kilometers.
4. It is not unlikely that the species with the greatest ranges are the oldest.
5. The relatively small differentiation in ecological preferences between the species gives an indication that the causes of speciation in the genus Orthodontium should be sought in phenomena other than in adaptation to different habitats.

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The author is glad to express his sincere feelings of appreciation for the cooperation experienced in this study from several botanical institutes and from a number of bryologists all over the world. Thanks are due to the directors and the curators of the Cryptogamic Departments of the herbaria of Helsinki (H), Stockholm (S), Geneva (GB), Paris, Laboratoire de Cryptogamie (PC), Brussels (Br), British Museum (BM), Kew (K), Leiden (L), the Farlow Herbarium, Cambridge, Mass. (FH), Washington, D.C., Smithsonian Institution (US), New York Botanical Garden (NY), Chicago, Field museum (F), Pretoria, Nat. herb. (PRET), Sydney, Nat. herb. (NSW), Melbourne (MEL) and Wellington, N.Z. (WELT).

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REFERENCES

Agsteribbe, E., J. J. Barkman, W. D. Margadant, W. Meijer, V. Westhoff, U. Witt (1950), Mosvondsten in Nederland. Ned. Kruidk. Archief, 57: 281—312.

Allorge, P. (1931), Sur quelques types de disjonction dans la flore muscinale ibérique. Travaux cryptogamiques dédiés à Louis Mangin, Paris, p. 465—475.

Allorge, P. (1934), Notes sur la flore bryologique de la Peninsule ibérique. Rev. bryol. N.S., 7, 249—301.

Allorge, P. & I. Thériot (1931), *Orthodontium gaumei* sp. nov. Rev. bryol. N.S. 4, 194—6.

Bartram, E. B. (1939), Mosses of the Philippines, Phil. Journ. of Science, 68 (1/4): 1—423; 29 plates.

Brotherus, V. F. (1909), Bryales, In Engler and Prantl, Die natürlichen Pflanzenfamilien, 10. Leipzig (1st ed., 2nd ed. 1925).

Burrell, W. H. (1926), Note on *Orthodontium*, Rep. British Bryological Soc. 2, 57.

Burrell, W. H. (1940), A field study of *Orthodontium gracile* (Wilson) Schwaegrichen and its variety *heterocarpum* Watson. Naturalist, London, no. 785, 295—302.

Cain, Stanley A. (1944), Foundations of Plant Geography. New York.

Dixon, H. N. (1924), Student's Handbook of British mosses, 3rd ed. Eastbourne.

Dixon, H. N. (1926), Studies in the Bryology of New Zealand. New Zealand Inst. Bulletin, no. 3: 198.

Dozy & Molkenboer (1844), Musci frond. archip. ind.: 19. Ann. Sciences Naturelles, III, série, Bot. Tom. II: 313. Musci frond. inediti ex archip. indico et Japoniae, Leiden.

Fleischer, M. (1902—1922). Die Musci der Flora von Buitenzorg. Bd. II (1904) contains descriptions of species of the genus Orthodontium.

Fulford, Margaret (1946), The Genus *Bazzania* in Central and South America. Waltham, Mass.

Gaume, R. (1932), Une espèce nouvelle de Mousse en forêt de Fontainebleau: *Orthodontium gaumei* Allorge et Thériot. Bull. de l'Ass. des Naturalistes de la Vallée du Loing, 15: 109—111.

Good, R. (1947), The Geography of the flowering plants. London.

Herzog, Th. (1925), Theorie und Tatsachen der Moosverbreitung und die Rolle des Peristomapparatus. Flora, N.F. Bd. 19: 198—226.

Herzog, Th. (1925), Die Moose Südbrasiliens als geographische Zeugen. Schröter Festschrift. Veröffentl. des Geobot. Instit. Rübel in Zürich. 3. Heft, p. 519—39.

Herzog, Th. (1926), Geographie der Moose. Jena.

Hooker, J. D. and W. Wilson (1844), Musci Antarctici. The London Journal of Botany. Vol. III: 533—556.

Hooker, J. D. and W. Wilson (1848), Icones Plantarum. Vol. IV, New Series Tab. 739 A (*Weissia pallens* Hooker, f. et Wilson) and B (*Orthodontium sulcatum* Hooker, f. et Wilson).

Hooker, W. J. (1837), Icones Plantarum. Vol. I, London.

Huxley, J. (1940) c.s., The new systematics. Oxford.

Huxley, J. (1942), Evolution, the modern synthesis, London.

IRMSCHER, E. (1923), Pflanzenverbreitung und Entwicklung der Kontinente. II. Mitt. Inst. allgem. Botanik, Hamburg.

KOPPE, F. and K. (1940), *Orthodontium germanicum* nov. spec. in Brandenburg. Fedde, Repertorium, Beiheft CXXI, 40—47.

LE ROY ANDREWS, A. (1932), The Californian Stablerias. Bryologist, 35: 49—51.

LE ROY ANDREWS, A. (1935), Bryaceae in Grout, Moss flora of North America, North of Mexico, II (3): 184—210.

LE ROY ANDREWS, A. (1950), Studies in the Bryaceae. II. *Orthodontium gracile* (Wilson) Schwaegrichen. The Bryologist, Vol. 53 (2): 117—118.

LINDBERG, S. O. (1878), Utkast till en naturlig gruppering av Europas bladmossor. Helsingfors.

LOTSY, J. P. (1928), On hybrid gones and homozygous hybrids. Annales bryol. I: 133—139.

MALTA, N. (1926), Die Gattung *Zygodon* Hooker & Taylor. Riga.

MARGADANT, W. D. & W. MEIJER (1950). Preliminary remarks on *Orthodontium* in Europe. Transactions. British Bryol. Soc., vol. 1 (4): 226—274.

MAYR, E. (1942), Systematics and the origin of species.

MEIJER, W. (1948), La flore des bryophytes du Lac de Naarden. Rev. bryol., N.S. 17: 101—118.

MEIJER, W. (1951), The recent distribution and the methods of propagation of *Orthodontium lineare* Schwaegr. Rev. bryol., T. 20, fasc. 1—2: 108—111.

MITTEN, W. (1856), A list of the musci and hepaticae collected in Victoria, Australia, by Dr F. Müller. Hookers Journal of Botany and Kew Gardens Miscellany. Vol. 8.

MITTEN, W. (1869), Musci Austro-Americani. Journ. of the Linn. Soc. Botany, vol. 12: 238—275.

MITTEN, W. (1883), Australian mosses. Trans. and Proc. Royal Soc. of Victoria, 19.

MITTEN, W. (1885). Voy. H. M. S. Challenger, Bot. IV.

MÜLLER, C. (1898), Symbolae ad Bryol. Australiae II. Hedwigia 37: 76—171.

MÜLLER, C. (1901), Genera Muscorum frondosorum. Leipzig.

PARIS, E. G. (1905), Index bryologicus. Ed. Sec. Vol. 3, p. 315—317.

PERSSON, H. (1944), On some species of *Aloina* with special reference to their dispersal by the wind. Svensk. Bot. Tidskr. 38 (3): 260—268.

PETTERSSON, BROR, (1940), Exp. Unters. über euanemochore Verbreitung der Sporenpflanzen. Acta Bot. Fenn. 25.

POTIER DE LA VARDE, R. (1950), Sur la persistance en Finistère de *Stableria gracilis*. Rev. bryol. Tom. 19 (1/2): 7—10.

REIMERS, H. (1941), Über *Orthodontium germanicum* F.u. K. Koppe. Notizb. Bot. Gart. Berlin, 15, no. 3.

RODWAY, L. (1913), Tasmanian Bryophyta. Part. III. Papers of the Royal Soc. of Tasmania. p. 177—263.

SCHIMPER, W. P., P. BRUCH & TH. GÜMBEL (1844), Bryologia europaea, 4: 330. Stuttgart.

SCHWAEGRICHEN, F. (1827), Species Muscorum, Suppl. 2, Sect. 2, p. 123—125.

SIM, T. R. (1926), The bryophyta of South Africa. Trans. Roy. Soc. S. Afr. 15.

STEBBINS, G. L. (1950), Variation and Evolution in Plants. New York.

TROLL, C. (1948), Der asymmetrische Aufbau der Vegetationszonen und Vegetationsstufen auf der Nord- und Südhalbkugel. Bericht über d. Geobotan. Forsch. Inst. Rübel: p. 46—83.

TUOMIKOSKI, R. (1940), *Calliergon megalophyllum* Mikut. und *Drepanocladus capillifolius* (Warnst.) Warnst. in Finnland. Annales bot. soc. Zool.-Bot. Fenn. Vanamo. Tom. 15 (3).

TUOMIKOSKI, R. (1949), Über die Kollektivart *Drepanocladus exannulatus* (Br. eur.) Warnst. Ann. bot. soc. Zool-bot. Fenn. Vanamo. Tom. 23 (1): 1—44.

VERDOORN, FR. (1934), Studien über Asiatische Jubuleae. Mit einer Einleitung: Bryologie und Hepaticologie, ihre Methodik und Zukunft. Ann. bryol. Suppl. vol. IV. The Hague.

VERDOORN, FR. (1945), The Plant scientist in the world's turmoils. Introd. Essay in "Plants and Plant Science in Latin America", Waltham, Mass.

VERDOORN, FR. (1950), The future of exotic cryptogamic Botany. The Bryologist, 53, 1: 1—9.

WALSH, H. (1951), *O. lineare* Schwaegr. Note in Trans. Br. Bryol. Soc. I (5), p. 488.

WATSON, W. (1922), A new variety of *Orthodontium gracile* Schwaegr. Journ. Bot. London, 60: 139—141.

WILSON, W. (1839), Suppl. Eng. Bot. vol. III. Table 2835.

WETTSTEIN, F. VON (1932), Genetik. p. 233—272. Manual of Bryology. Ed. Fr. VERDOORN, The Hague.

WETTSTEIN, F. VON (1942), Über einige Beobachtungen und experimentelle Befunde bei Laubmoosen. Ber. Deutsche Bot. Ges. Bd. 60: 394—414.

WULFF, E. V. (1943), An introduction to historical Plant Geography. Waltham, Mass.

FLOWER COLOURS AND THEIR FREQUENCY

BY

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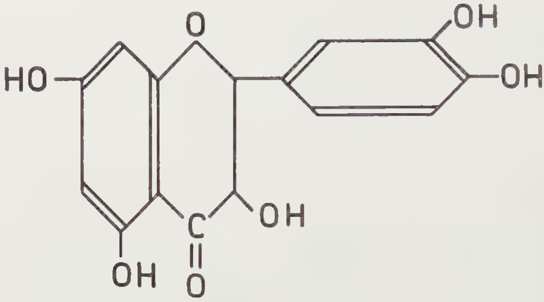
Flower pigments are among the easiest recognisable chemical characteristics of plants, although it is unfortunately not possible to analyse them by sight. The former circumstance induced me to study the frequency of flower colours in a number of widely different countries. It was my intention to take into consideration as many species as possible also those from the tropics. Consequently I was not able to give biochemical or genetical surveys such as those of ROSE SCOTT-MONCRIEFF (15) or of T. WIT (19) and could only take into account the colour data mentioned in the standard flora's in question. The adoption of this method involved certain difficulties since the problem is not so simple as was formerly supposed when it was customary to speak of one single pigment, anthocyan, which when dissolved in cell-sap at a low p_H would be red and at a high p_H blue. Things are by no means so simple, as we shall see later on.

The following colours were distinguished: (1) green, (2) white, (3) yellow-orange, (4) pink-red in different tones, (5) purple, (6) violet-lilac, (7) blue.

Green parts of plants, also the young flowerbuds contain the same pigments as the leaf, viz. two green pigments, chlorophyll A & B, besides two yellow-orange ones, carotene ($C_{40}H_{56}$) and xanthophyll, 3,3-dioxy-α carotene ($C_{40}H_{56}O_2$). These green and yellow pigments are not soluble in water but carried by plastids.

The white parts of the flowers contain no pigments whose solution in the cell-sap is perceptible to the human eye. The total reflection caused specially by air-containing intercellulars of the corolla brings about a white colour. The restriction, perceptible to the human eye, must be added because most or perhaps even all those flowers which we call white contain a kind of anthoxanthins, compounds which when solved in water absorb in the near ultraviolet only. To bees whose eyes are insensitive to red radiation but sensitive to that in the near ultraviolet the presence or absence of such anthoxanthins must be perceptible. HALDANE (2) maintains that this kind of anthoxanthins is present in all white flowers. The fact that red poppies are visited by bees is due to the presence of these compounds.

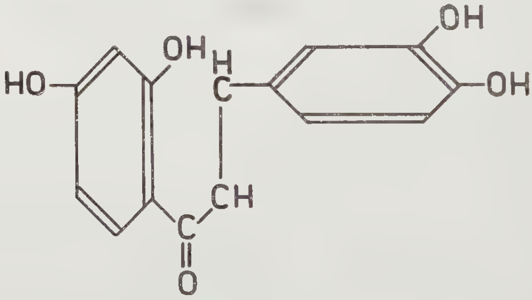
Yellow or orange flowers contain carotenoids as was proved long ago by T. TAMMES (16). In tomato fruits an isomere of β-carotene, called lycopene is to be found, in yellow flowers e.d. Viola spec. different epoxides which are also insoluble in water. In flowers sometimes yellow water-soluble pigments of a totally different chemical constitution however, are met with which are anthoxanthins. These compounds, flavones and flavonols



FLAVONOL (QUERCETINE)

are usually present in glycosidic form, in combination with one or two molecules of a sugar. First studied by Perkins (11) they were later on an object of special study by P. Karrer (3) as well as by the Robinson's (14) and by Price (13).

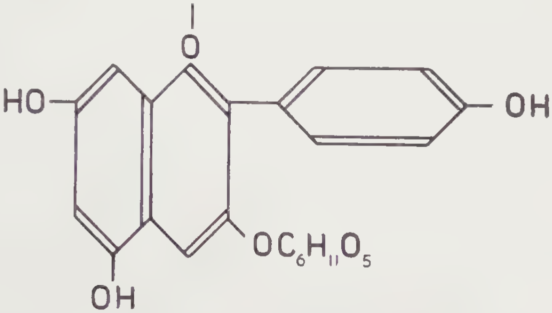
The chemical relation of anthoxanthins and anthocyanins will be dealt with later, here however I will mention that Price isolated the chalcone butein from the yellow flowers of *Dahlia variabilis.*



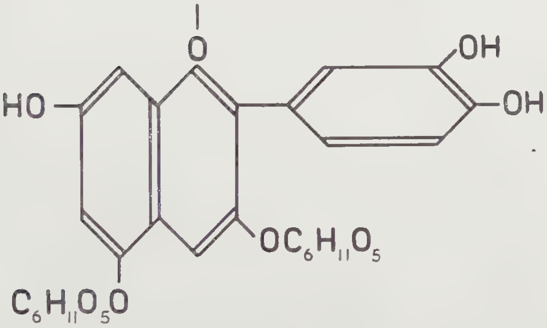
CHALCONE (BUTEIN)

The red and blue colours of flowers are caused by anthocyanins which are also glycosides, the aglycone anthocyanidin being combined with one or two sugar molecules. If this sugar is a monose the glycoside is in the former case called a monoside, in the latter a dimonoside. The anthocyanidins are to be derived from the hydroxyflavilium compounds pelargonidin, cyanidin and delphinidin which differ in number of hydroxylgroups.

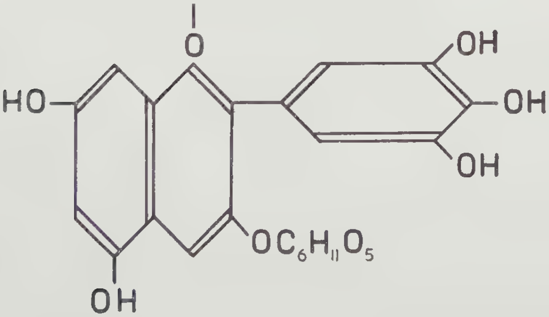
Pelargonidin has only one, cyanidin two and delphinidin three hydroxyl groups in the 2- phenyl nucleus. The hydroxylgroups can be methylated, so there is one methylated derivative of cyanidin called peonidin and three of delphinidin called petunidin, malvidin and hirsutidin. Some twenty anthocyanins are isolated from the higher plants and some of them e.g. hirsutidin, trimethyldelphinidin seem to be characteristic of special genera.



PELARGONIDIN 3 MONOSIDE



CYANIDIN 3.5 DIMONOSIDE



DELPHINIDIN 3 MONOSIDE

Combinations of these anthocyanins may be even characteristics of families of the Phanerogams. In this respect I refer to my publication (18) on the relation between taxonomy and chemistry in plants.

The number of these hydroxylgroups is one of the factors upon which variation in colour from bright red to purple depends; an increase of this number causes an increasing tinge of blueness. On the contrary methylated anthocyanins are redder than the corresponding unmethylated ones, whilst dimonosides are bluer than monosides of the same anthocyanidins.

Variation in colour also depends upon changes in p_H of cell-sap, an increase in p_H causes increase in blueness. In the opinion of LAWRENCE and PRICE (7) the influence of the latter factor however, is not so dominating as was formerly supposed. The cell-sap of blue corn-flowers turns blue-litmus red and is more acid than that of red roses which contains the same anthocyanin. If this opinion of LAWRENCE and PRICE holds good there must be yet another factor which causes the purely blue colour to arise. The difference in colour e.g. between young flowers of *Anchusa italica* and full-grown ones of the same species is not caused by a different p_H- value. In most Boraginaceae the blue-flowering species have red flowerbuds, in the Scrophulariacea *Polycarena discolor* the young flowers are blue, the adult ones rosy. The studies of the ROBINSONS' (14) have shown on the one hand the influence of the colloidal condition of the cell-sap, on the other hand the significance of so-called co-pigments. These substances, colourless anthoxanthins or tannins effect the colour of anthocyanin-solutions, making them pure blue by the formation of loose compounds. Even with a p_H 4,9 the colour may then be a pure blue one, e.g. the blue colour of cornflowers, caused by the diglycoside of cyanidin. In 1939 the ROBINSONS' suggest absorption of the cyanin to colloidal polysaccharids.

From a chemical point of view the anthocyanins and anthoxanthins are closely related and several authors have argued in favour of a synthetical interrelation. Formerly WHELDALE ONSLOW (9) supposed that anthocyanins were oxidation products of flavones and flavonols, but later on when their chemical constitution was better known this theory was discarded in favour of a reduction process. The ROBINSONS' who have given us the most important contribution in this matter suggest that both kinds of substances, anthocyanins as well as anthoxanthins may be derived from the same intermediate. The latter might be built up from two hexose-units and one aldose unit by a series of aldol-condensations. This theory can be supported by general observations of competition in development between these compounds, particularly in flowers of *Dahlia variabilis*, although the yellow substance here is not a real anthoxanthin but a closely related compound a chalcone (s. formula). This theory might also give the explanation of a fact observed by WHELDALE ONSLOW & BASSETT (10), who showed that crossing of an ivory-yellow variety of *Antirrhinum majus* and a white-coloured one produced a magenta-red offspring. The genetic side of the question can not be dealt with here.

In the following table only the colours of the corolla, perianth or coloured calyx are taken into account, not those of the bracteae. When the stamens or their filaments are responsible for the colour, as is often the case in Myrtaceae, these colours were also taken into account. Species with flowers without a well developed corolla and calyx, such as those of Gramineae, Cyperaceae, or Cupuliferae were not recorded. On the other hand it was necessary to record species with two or more colours in their flowers under several heads. I have adopted the same course with Compositae, having differently coloured ray- and disk florets, or with species frequently giving colour varieties. The number of recorded cases was thus always greater than that of the species concerned, mostly in the ratio of appr. 125 : 100. Tints such as violet-blue were recorded as blue, whilst blue-violet was recorded as violet. The data are percentages from each total number of cases.

The examined flora's were those of the following countries:

(1)	the Netherlands	by Heukels and Wachter
(2)	France	by Bonnier and de Layens
(3)	Switzerland	by Gremli
(4)	Sweden	by Lindman
(5)	Victoria (Australia)	by Ewart
(6)	Tropical Africa	by Oliver
(7)	Cape Colony	by Thiselton Dyer
(8)	Java	by Backer

TABLE 1

colour	Average	Scandinavia	Netherlands	France	Switzerland	Sweden	Victoria	Trop. Africa.	Cape Col.	Java
green	7½	0,8	7½	6½	6½	8	9	8	7	7
white	26½	1,4	26½	26½	26	26	27	26	25	30
yellow	31	1,8	32	31	31	33	33	27	32	30
red-pink	15	1,4	15	18	16	13	15	15	16	15
purple	7 } 29	2,8 } 1,9	7 } 29	4 } 30	6 } 29	4 } 28	7 } 26	12 } 33	11 } 31	5 } 30
violet	7	2,4	7	8	7	11	4	6	4	10
blue	5½	1,1	5½	6	7	6	5	6	5	3
total										
species[1]	22850		1000	2375	1825	1350	1750	5500	7150	1900
cases	28150		1200	3000	2200	1530	2270	6600	8900	2450
percent.	123		120	126	121	114	130	120	124	129

[1] appr. 18000 different species

A drawback was that in the flora of Tropical Africa colours of flowers often were not mentioned, whilst Backers' Flora of Java is not yet wholly completed. The species introduced in Java by man are not recorded.

On examining the table one is struck by the fact that there is such a large measure of agreement between the data of widely different parts of the world. The low values of the standard deviations are evidence of of this fact. Not only are the differences between the countries of Western Europe inconsiderable but the same is true as regards the data of Tropical Africa, Cape Colony and Victoria. Java is somewhat an exception, but the incompleteness of the flora may be the cause of this. It is especially the standard deviations for white, yellow, green and blue, that are small, those for purple and violet are greater. One of the causes of this fact is that the same species are in one flora recorded as having red flowers, in another as having purple ones. If we take red, purple and violet together the agreement is closer, (Average 29, Standard Deviation 1,9).

If there are differences in colour frequency between countries and climates they cannot be so great as has often been maintained.

With respect to red and blue colours the question of differences in connection with the surroundings will be entered into later. First however, it is necessary to point out that the predominance of yellow and white colours in parts of Western Europe, e.g. in our Dutch meadow-landscape is only partly to be ascribed to the greater number of species with flowers of these colours. For the yellow colour this amounts to 31 %, for the white colour to 26½ %, together not more than 57½ %. Next to this the fact is to be observed that some of the yellow- or white-flowering species have by far the greatest number of individuals. As a matter of fact we must not forget that on the moors and bogs of Western Europe the dominating flower-colour is a whitish pink or violet.

We are coming now to a discussion of the red and blue flower-colour and it is obvious that the vegetative parts also must be discussed in this connection. Blue colours are not frequent in vegetative parts and are only to be met with in bracteae of the floral region e.g. *Ajuga, Bartsia, Bromeliaceae.* On the contrary red colours are very often present in vegetative parts, leafs, stems etc. and the connection of these pigments with those in the flowers was accentuated by LAWRENCE and PRICE (7). The authors proved that in vegetative parts the same anthocyanins are met with as are mentioned above for the flowers. There is only one remarkable difference viz. the marked preponderance of cyanidin. Of the plants examined the number of genera containing cyanidine-derivatives expressed as a percentage of the total number of genera examined is: in autumn leaves 95 %, young leaves 93 %, permanently pigmented leaves 76 %, fruits 69 % and flowers 50 %. The authors come to the conclusion — which might be supported by the chemical structure of the compounds in question — that cyanidin is the anthocyanidin originally formed, which by mutation might give pelargonidin or delphinidin, the former by reduction, the latter by oxidation. The opinion of LAWRENCE and PRICE l.c. is, that selection has been an eliminating factor, as in the tropics by far the greater part of the flowers which contain pelargonidin is to be found.

Pollination by bees dominates in temperate regions, whilst in the tropics birds and butterflies are of preponderant influence. Nor should it be forgotten that VAN DER PIJL (12) has shown that purple flowers with a definite odor have a special attraction for bats, which are then the pollinating agents. The selective influence might be understood by consideration that pelargonidin-derivatives are more reddish, delphinidin-derivatives more blueish and that bees are sensitive to blue and ultraviolet rays whilst on the contrary birds, butterflies and bats are sensitive to red and purple. The supposed selective value of these facts however, is rarely proved and sometimes rather exaggerated. The data of the preceding table are not very convincing in this respect. The flora of Java — apart from the species introduced by man — does not show preponderance of red flowering species in general, only of the violet-lilac ones. It should also be borne in mind that without co-pigments the colours of the anthocyanins in living tissue vary from bright red to purple, not to blue.

It has been pointed out frequently that the temperature of environment directly influences the production of colour in flowers, especially of the blue colour. KLEBS (5) observed a change in flowers of *Campanula Trachelium* from white in the hothouse to blue in a cold environment. He ascribed this fact to a more rapid growth in the former case which would lead to insufficient material for anthocyan-production. This eplanation does not tally with observations by KUILMAN (6) with germinating plants of *Fagopyrum esculentum*. At a temperature of 25° C. production of the anthocyanidin—cyanidin.3 according to KARSTENS (4) — takes place more quickly but the total quantity is smaller than at 5° C. In KUILMAN's opinion this process consists of two separate ones, a purely chemical and a photochemical one. By illumination a chromogen is formed from a prochromogen and this process takes place the more quickly as temperatures are higher. In other words the photochemical reaction is accompanied by a chemical one with less velocity. The second part of the anthocyanin production — change of the chomogen into anthocyanin — is an ordinary dark-reaction but there temperature has the peculiar effect which was mentioned above. At a lower temperature the total production is higher, a fact which might be explained by assuming that at high temperature this chromogen is changed into a different compound. In young leaves as well as in autumn leaves an explanation of the production of anthocyanin might be found in this manner. NOACK (8) associated this anthocyanin production with flavones and flavonols (s.above). He suggested that changes in the intensity of photosynthesis influenced the equilibrium flavonol $\rightleftarrows$ anthocyanidin by means of the changing oxygen tension. His views however, were not confirmed by KUILMANS' experiments.

This discussion was mainly concerned with anthocyanin production in vegetative parts. Whether the same reasoning is valid with respect to the production of these pigments in flowers is another question. Many observations e.g. by BONNIER (1) suggest that by stronger ultra-violet radiance at a higher level the formation of blue pigment in the flowers of mountain regions is intensified. A possible influence of the greater changes in day- and night-temperature is almost entirely neglected in spite of the observations of KLEBS l.c. VAN DER PIJL (12a) in these respects mentions an Ageratum species in Java. Besides the white coloured flowers also blue coloured ones are to be found in the low lying plains but only very seldom. As appears from an observation by E. Nijland both forms grew side by side at appr. 1000 m on the Pangerango but here the pure white ones are rare and have disappeared at appr. 1800 m. At a height of appr. 2400 m only deep blue flowers are to be met with.

These facts can be explained either by postulating the existence of two genetically different forms, a blue- and a white flowering one, of which the former predominates by selection especially at a higher altitude, or by accepting a direct physical-chemical influence on the colourproduction of one single form in connection with the altitude. Heredity experiments might settle the matter but the presence of white and blue coloured flowers side by side points towards the former alternative. In deed both explanations might be true.

What, generally speaking, are the flower colours of species on higher mountains? Are they different from those in the lower regions around them? In table II is compared:(1) the flora of Switzerland as a whole with the species of the Swiss Alpine mountain region above 1100 m (Alpen & Voralpen), both from the flora of Gremli. (2) the flora of Java as a whole (Flora of Backer, but without the species introduced by man) and the mountain flora of Java above 1500 m (Flora of Koorders).

The flora of Backer, as already was said, is not complete, but the missing families are not very important in connection with the question of blue and red flower colours in which we are mainly interested here.

TABLE 2

Colour	Switzerland Gremli		Java	
	total	above 1100 m	Backer total	Koorders above 1500 m
green	6½	5	7	9
white	26	23	30	36
yellow-orange	31	31	30	24
red-pink	16 }	15 }	15 }	14 }
purple	6 }29	4 }29	5 }30	4 }26
violet-lilac	7 }	10 }	10 }	8 }
blue	7	11	3	6
species	1830	380	1900	275
cases	2200	460	2450	320
percentage	120	121	129	116

In both cases, in Switzerland as well as in Java the differences in the frequency of red and blue-flowering specious are obvious. We observe a kind of shift from red to blue. In Switzerland the percentage of blue-flowering species rises from 7 % to 11 %. In Java where the percentage for the total island is extraordinarily low (3 %) it rises to the double value in the mountain region above 1500 m.

It is possible to put this fact differently. There are especially among the Sympetals genera with many species, the great majority of which possess blue coloured flowers e.g. *Campanula*, *Gentiana*, *Myosotis*, *Veronica*. It is a remarkable fact that many of these genera are to be found found especially in mountain regions and cause the high percentage of blue-flowering species.

It seems extremely doubtful whether direct influence of light and temperature might have caused this preponderance of blue-flowering species. Seeing that modifications are not hereditary, the development in question must have been due to mutation caused by climatic factors. Experimental evidence is almost entirely lacking however, although Russian authors as N. I. VAVILOV, claim that stronger radiation at high altitude promotes the mutability of species. Just as in other questions of evolution and descent the time factor places these developments beyond the range of experimental evidence.

The main point in the question of flower colours however, is the fact proved above that in totally different parts of the world the percentages of white-, yellow-, or red-flowering species are about 5 times as high as those of the blue-flowering ones. It is evident that the originating of all these species did not take place in the same circumstances and this fact in my opinion leads to the assumption that in the course of ages evolution of pigment in flowers has, generally speaking, been an autonomous genetic process. The process may be slightly influenced by environment, this word taken in the widest sense and including the pollinating agents. Though environment varied greatly in different parts of the world yet in this matter of flower colour the result of evolution has been almost the same. Only the mountain flora seems to be an exception.

I will wind up with a further discussion of this fact that the percentage of species with blue flowers is everywhere so low, 5½ %—7 %; the only observed exceptions being the mountain flora of the Alps, 11 % and that of Java 3 %.

Many years ago HUGO DE VRIES (17) gave the following suggestion: the yellow flowers might have arisen by loss of green pigment in the corolla whilst loss of both green and yellow pigments might have given a white corolla or perianth. Both were cases of retrogression, of the well known and common phenomenon of loss of character through mutation. Red pigments are present in almost every group of Phanerogams and formation of blue pigment might have taken place by mutations which in the opinion of DE VRIES were nothing but a change of the acid cell-sap into an alkaline one. This mutation was supposed to be a progressive one and as such much rarer then the retrogressive loss of green and yellow pigment.

This rather simple way of representing the facts cannot be maintained. In the first place because mutations which control formation of these pigments are usually much more complicated. In *Zea Mays* at least 11 different dominant genes must be present for the production of chlorophyll and carotinoids; in *Lathyrus odoratus* there are at least 13 genes affecting flower colour. In other cases the latter process is more simple as is proved by crossing experiments. These instances will suffice to show the intricacy of the question. But there is more to be said in this connection. An important group of yellow flowers contain anthoxanthins, the yellow, water soluble pigments which bear no relation at all to the carotinoids. Moreover a change of the p_H of the cell-sap although of importance with respect to the colour of anthocyanins is not the decisive factor in living tissues of plants. As was already said above the colloidal condition of cell-sap and the presence of co-pigments are said to be more decisive in the changing of red into blue.

According to Haldane (2) we cannot in general say that blueing genes are either dominant or recessive. This author distinguishes the following genes which cause blueing: (1) genes controlling acidity. This acidity is dominant of alkalinity, the blueing effect is recessive. (2) genes favouring co-pigment formation, generally at the expense of anthocyanin. In this case the blueing effect is dominant and sometimes accompanied by dilution of the anthocyanin, due to competition from the common source (s. above). (3) genes substituting a more oxidised and thus more blueish anthocyanin for a less oxidised and more reddish one; her blueing is always dominant.

It is generally known that there are many wild growing species with blue flowers which often give reddish or pink varieties e.g. *Aquilegia vulgaris*, *Delphinium consolida*, *Polygala vulgaris*, *Ajuga reptans*, *Salvia pratensis*, *Endymion nutans*. On the other hand there is perhaps only a single case in which a wild growing species with red flowers has a blue coloured variety. *Anagallis arvensis* s.sp. *coerulea* Voll. (forma *femina* Nills) might be an example but an equally possible view is the following. The genus *Anagallis* might be considered as having in general blue flowering species, e.g. *Anagallis Monelli* Clus., *Anagallis latifolia* L., *Anagallis grandiflora* Andr. so that the red-flowering species *Anagallis arvensis* is an exception, formed by a recessive mutation as in the cases mentioned above. *Anagallis arvensis* s.sp. coerulea might then be a case of degression or regression, the reassuming of activity by a latent character s. de Vries l.c.. Be this as it may, the numerous red or pink varieties of blue flowering species prove that we have here a case of recessive mutation, a so-called factor mutation in which a dominant factor changes into a recessive one. Even in vegetative varieties this can happen as was observed by Bateson in *Lathyrus odoratus* when an individual with violet flowers produced a branch with red ones.

According to these facts it appears likely that in the arising of red flowering varieties from blue-flowering ancestors it is the co-pigment factor which from dominant changes into recessive. Consequently the mutations which gave blue-flowering mutants from red-flowering species must have been progressive mutations in the sense of Hugo de Vries and very rare as such. Here in my opinion lies the explanation of the low percentage of blue-flowering species in all parts of the world, the same explanation as was suggested by de Vries, but argued in a different way.

Perhaps it is worth while to note the following facts compiled from the work of A. Karsch, called Vademecum botanicum. This book contains the species of the higher plants of Germany ,Western and

Central Europe besides the best known species of other countries of the world, in total some 9000 species. If we select from this Vademecum the genera in which blue-flowering species are to be found we get a number of appr. 180 genera with appr. 1170 species. Of these species 41 % have blue flowers, 11 % white-, 15 % yellow-, 10 % red-, 8 % purple- and 15 % violet ones. That this percentage of yellow flowering species is as high as that of the violet ones might give occasion for the suggestion that blue pigment can as well be formed in connection with a yellow as with a red pigment. Remembering what was said above about the chemical relation of anthocyanins and anthoxanthins we might suppose the yellow pigment in this case to be an anthoxanthin, which by progressive mutation might give the blue pigment.

SUMMARY

After a short survey of the chemical structure of flower pigments the relative frequency of the various flower colours is examined on the basis of an analysis of standard flora's of different parts of the world: The Netherlands, France, Switzerland, Sweden, Tropical Africa, Cape Colony, Java and Victoria (Australia). The following colours were distinguished: green, white, yellow-orange, red-pink, purple, violet-lilac and blue. In the flora's thus analysed the percentages of species with these flower-colours do not vary greatly, as is proved by the small standard deviation. The data are: green 7 ½% (St.D. 0,8), white 26½ % (St.D. 1,4), yellow-orange 31 % (St.D. 1,8), red-pink 15 % (St.D. 1,4), purple 7 % (St.D. 2,8), violet-lilac 7 % (St.D. 2,4), blue 5½ % (St.D. 1,1) Red, purple and violet taken together 29 % (St.D. 1,9).

The dominance of species with red flowers in the tropics, often supposed to be founded on selective action by birds, bats and butterflies is less pronounced in the table than usually claimed, whilst in the flora of Java it is lacking. A higher percentage of blue-flowering species in temperate regions is not borne out by the analysis either. But there is a marked difference as regards percentages of blue-flowering species between the flora of Switzerland as a whole and that of the Swiss Alpine mountain region above 1100 m. The respective percentages are 7 % and 11 %. In the flora of Java which as a whole has a very low percentage of blue flowering species (3 %), this percentage in the mountain region above 1500 m is 6 %.

In connection with the experiments of KLEBS and others the idea of a direct influence of radiation cannot be ruled out entirely although its significance for the originating of new species is very problematic. Russian authors (N. I. VAVILOV) have claimed an influence of more intense radiation in high altitude on mutation processes. The possibility of selection by pollinating agents (*2a*) deserves consideration, decisive experiments in this matter however, are almost lacking.

The main point in the question of flower colour is the fact established by an examination of some 18000 different species from

various parts of the world, that in these countries the percentages of white-, yellow-, or red-flowering species are almost everywhere about 5 times as high as that of the blue-flowering species. The mountain-flora is the only exception. This fact leads us to the assumption that in the course of ages the evolution of blue pigment in flowers has been an autonomous genetic process only slightly influenced by environment and by the selective action of pollinating agents.

This genetical problem of colour evolution in flowers is discussed and the conclusion, corresponding with DE VRIES' suggestion, is that whilst yellow flowering as well as white flowering species may be originated by retrogression, the arising of blue-flowering species from red flowering ancestors must have taken place by progressive mutations, in casu of the co-pigment factor. In the fact that these progressive mutations are much rarer than retrogressive ones lies in my opinion the explanation of the low percentage of blue flowering species in all parts of the world.The frequently observed phenomenon of wild blue species giving pink coloured variants is a case of factor mutation in which a dominant factor, probably the co-pigment factor, changes from dominant into recessive.

Amersfoort 1951

REFERENCES

1. BONNIER, C., Ann. Sc. nat. 7 Ser. T 20 (1896.
2. HALDANE, J. B. S., New Paths in Genetics (1942).
2a. HUXLEY, I. S., Evolution. (1942).
3. KARRER, P., Plant Pigments Ann. Rev. Biochem. (1932/33).
KARRER, P. and JUCKER, E., Carotenoids (1950) came too late to my notice to be considered.
4. KARSTENS, W. K., Thesis Leiden (1938).
5. KLEBS, G., Jahrb. f. wiss. Bot. 42, (1906).
6. KUILMAN, K. W., Rec. d. trav. bot. néerl. 27, (1933).
7. LAWRENCE, W. J. C. & PRICE, J. R., Biol. Review 15, (1940).
8. NOACK, K., Zeitschr. f. Bot. 14, (1922).
9. ONSLOW, M. WHELDALE, Journ. Genet. 1, (1911).
10. ONSLOW, M. WHELDALE, & BASSET, H. L. Biochem. Journ. 7, (1913).
11. PERKINS, A. J., Journ. Chem. Soc. 95, (1910).
12. PIJL, L. VAN DER, Plantenleven in Indië.
12a. PIJL, L. VAN DER, Plantenleven in Indië.
13. PRICE, J. R., Biochem. J. 32, (1938).
14. ROBINSON, G. M. & ROBINSON. R., Biochem. J. 25, 26, (1931/32).
15. SCOTT-MONCRIEFF, ROSE., Journ. Genet. 30, (1936).
16. TAMMES, T., Flora 87, (1900).
17. VRIES, HUGO DE., Die Mutationstheorie (1903), Species and Varieties, their Origin by Mutation (1906).
18. WEEVERS, TH., Blumea, 5, (1943).
19. WIT, TH., Thesis Groningen, (1936).

REDUCTION OF TWO ENDEMIC MONOTYPIC PAPUAN GENERA

BY

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1. Lamiofrutex Lauterbach = Vavaea Bth. (Meliaceae)

Among the rather numerous monotypic endemic genera described from New Guinea there are some of which the position is doubtful. One of them is *Lamiofrutex* Lauterbach (Nova Guinea 14 : 147. 1924) referred by its author to the Rutaceae, presumably on account of its pellucid-dotted leaves. Engler (Nat.Pfl.Fam.ed.2, 19a : 330. 1931) had little hesitation to insert it in the Aurantioideae next to *Atalantia*.

The plant of which authentic material is preserved both at Bogor and Leiden appears to represent a species of *Vavaea*, of the Meliaceae.

I have compared it with 14 of the 16 species described, and I cannot reduce it to any of them; apparently it represents an unknown species. Its specific epithet papuanus cannot be used in Vavaea on account of *V. papuana* F. M. Bailey. It is therefore renamed here: **Vavaea lamii** nom.nov. — *Lamiofrutex papuanus* Laut. Nova Guinea 14 : 147. 1924.

Among the Vavaeas it is distinguished by thin leaves, absence of

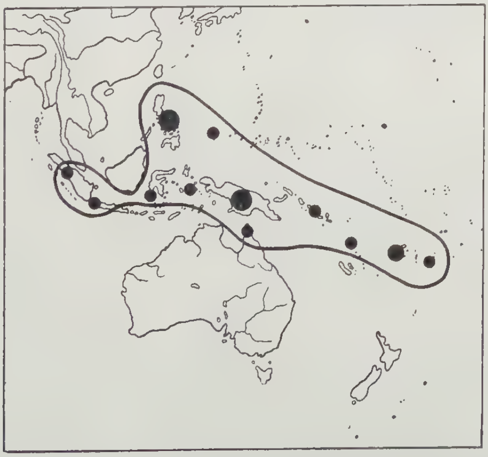

Fig. 1. Distribution of the genus Vavaea; the Philippines and New Guinea possess ca. 5 spp. each, Fiji 3, the other dots represent the occurrence of one species or one locality.

indument, a nearly entire staminal tube, and its habit which is that of an unbranched 1 m high shrub. Specific distinction in this genus is difficult, and many reductions may be expected by a future revisor.

Notwithstanding the rather large number of species, specimens are few and apparently rare. The richest centres of development (in described species) are New Guinea and the Philippines. The area of distribution is gradually becoming clear and I have drawn it on the accompanying map. As with several genera which are now known as largely Malaysian, the first species described was from the margin of the area viz *V. amicorum* Bth. from the Tonga group, E of Fiji, the easternmost extension of the genus. In West Malaysia there is still a gap in the area by the absence of Vavaea in Borneo; it may be expected to occur there (fig. 1).

2. Classification and revision of the genus Nouhuysia (= Idenburgia), family Guttiferae.

In 1939, while checking some generic names of Papuan plants, I found that *Nouhuysia* Lauterbach described in the Guttiferae (1912) and *Idenburgia* Gibbs (1917) referred to the Monimiaceae are identical.

According to a private communication (May 1951) Dr J. G. B. Beumée had independently reached a similar conclusion earlier.

The position of *Idenburgia* in the Monimiaceae has been connected with that of *Trimenia* and *Piptocalyx*. Miss Gibbs was convinced of this alliance although she regarded both genera as anomalous in the family in her earlier work and established a separate tribe for them, and later (1917) a separate though allied family Trimeniaceae in which she also included Idenburgia on the strength of anatomical characteristics.

L. Mooney, I. W. Bailey & B. G. L. Swamy (Journ.Arn.Arb. 31 : 373, 395. 1950) in their thorough anatomical study of the Monimiaceae keep both families Monimiaceae and Trimeniaceae separate, but have come to the conclusion that Idenburgia does not belong to either of them.

Hitherto there has been no doubt about the placing of *Nouhuysia* in the Guttiferae, and a closer examination has confirmed this, mainly by the absence of the pellucid-punctate balsam cells typical of Monimiaceous leaves and the presence of short, but distinct resinous ducts in the young leaves and tepals, both characters hitherto not described.

Within the family Guttiferae *Nouhuysia* occupies a rather separate position, specially in its habit: leaves spread but pseudo-whorled on the nodes (similarly to those found in many other genera e.g. *Daphniphyllum*, *Drimys*, *Pittosporum*, *Terminalia*, etc.) which are distinctly glandular-dentate.

Engler (Nat.Pfl.Fam.ed.2, 21 : 169 seq. 1925) placed it in the tribe Calophylleae, but this seems definitely erroneous. In determining *Nouhuysia* with Engler's system one arrives closer to the Formosan genus *Owataria* Matsumura (Bot.Mag.Tokyo 14 : 1. 1900) in the tribe Clusieae. Besides being entirely different in floral structure, this genus seems to be doubtful in the Guttiferae since Gagnepain

(Fl.Gén.Indochine 5 : 426. 1926) has reduced it to the Euphorbiaceous *Gelonium*, a reduction which needs corroboration.

In my opinion *Nouhuysia* is undoubtedly representing a separate tribe of the Guttiferae which I will name:

Tribus *Nouhuysieae*, trib. nov. Guttiferarum. Folia sparsa vel ± pseudoverticillata ad nodos, margine glanduloso-dentata. Racemi terminali; segmenta perianthii 4, dimera, caduca. Antherae elongatae, 6—12 uniseriatim dispositae, longitudinaliter dehiscentes. Ovarium 2-loculare, ovulum 1 pro loculo, ab apice pendens. Drupa 2 vel 1 seminata, interiore ruminata.

Typus: *Nouhuysia* Laut. Nova Guinea 8^4 : 843. 1912.

The examination of the pollen of *Nouhuysia* was kindly executed by DR G. ERDTMAN, Director of the Palynological Institute at Stockholm. He shares my opinion about the status of *Nouhuysia* in Guttiferae; he finds a few features in common with *Montrouziera* and *Symphonia*, from New Caledonia and Madagascar respectively. His diagnosis of the pollen of the specimen KOSTERMANS 2198, dd. 6/6/51, runs: Pollen grains 3-porate, oblate (14.5 × 20.5 μ). Exine 1.5 μ thick. Sexine thinner than nexine, tegillate, faintly baculate; pattern ± obscure. Pore diameter about 3 μ. Grains ± circular in polar view, ± rectangular (with thin, depressed, slightly irregular polar areas) in equatorial view.

As to the demarcation of the species it is clear that *Nouhuysia papuana* Laut. has been redescribed in *Idenburgia*, and a thorough investigation has resulted in the distinction of only 3 species by reducing 3 other names to synonymy. Of *N. arfakensis* Gibbs I had no material but a recent collection in the type locality by DR KOSTERMANS has furnished excellent material entirely fitting the type description and figure. I have also not seen type material of *I. pauciflora*, but according to DR SMITH's full description it is a marked species. Of all other types I could examine type material as DR BEUMÉE had formerly secured fragments of the types for the Bogor Herbarium at Berlin.

The following general remarks are made on the variability.

(1) Indument. The indument in *N. papuana* Laut. is very scarce. The inflorescence is slightly hairy becoming glabrescent with age. But in several specimens the hairs on rhachis and pedicels have been replaced by minute brown scurfy scales. In one sheet (KOSTERMANS 2198) I found both types of indument in one number. This is apparently a case similar to some others I found in Javan *Rhododendron* and in *Aglaia* where in one species a hairy or lepidote indument can occur. The occurrence of some ciliae on the tepals is of no importance, all intergrades to glabrous ones occur.

(2) Floral bracts. In *N. papuana* the bracts are early caducous, but young inflorescences have a strongly strobiloid appearance resembling that of *Trimenia* and *Piptocalyx*, to which resemblance adds the slightly carinate midrib (through pressure?) of bracts and outer tepals. Such bracts are not found in *N. arfakensis* as far as the material permitted to observe.

(3) Tepals. The two outer tepals are distinct from the 2 inner

by their slightly saccate solid base. One could accept them to represent large bracteoles.

(4) Third whorl of tepals. The occurrence of a third whorl of tepals is mentioned and figured for a specimen described by Gilg & Schlechter as *I. pachyphylla*. The occurrence of these lanceolate-oblong segments seems occasional. In the dozens of flowers which I dissected I found only once one such segment (Pulle 681) and that was obliquely placed and not decussate as pictured by Gilg & Schlechter. It did certainly not belong to the staminal whorl but could well be imagined to represent a staminode of a potential second staminal whorl.

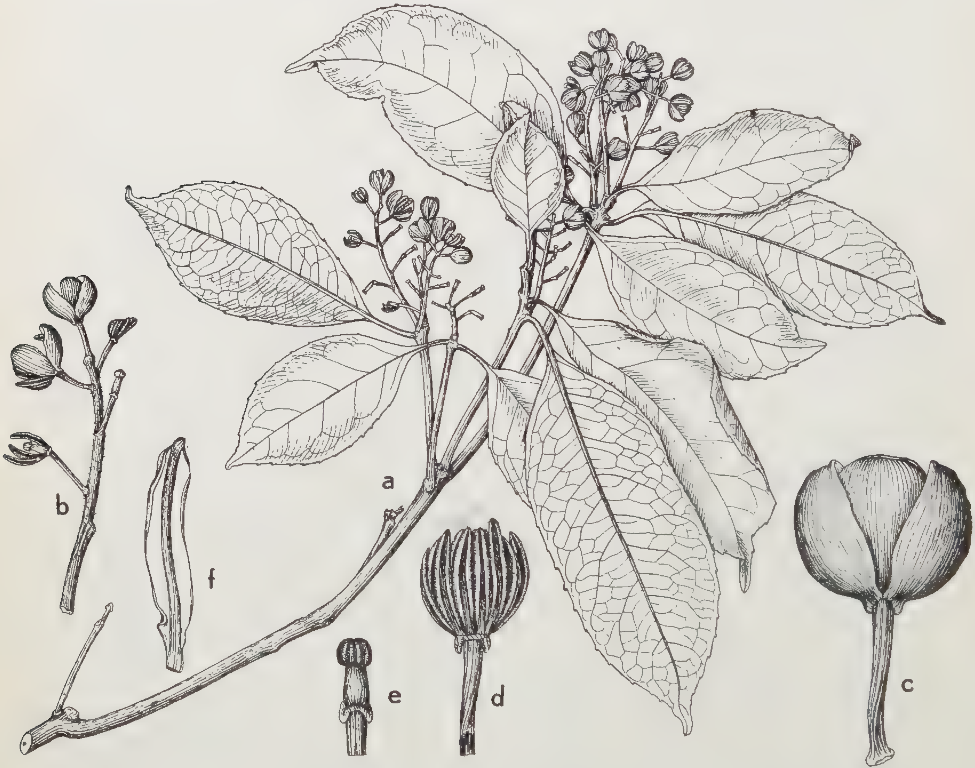

Fig. 2. Nouhuysia papuana Laut. (after Rutten 2240 from Ceram). *a.* flowering twig, × $^1/_2$, *b.* inflorescence, nat. size, *c.* ripe bud, × 3, *d.* flower during anthesis, × 3, *e.* pistillum, × 3, *f.* anther dorsal side, × 5.

(5) Stamens. The stamens in all specimens are much alike and the androecium certainly has the aspects of the Trimeniaceae. The number is in *N*, *arfakensis* 6, and in *N. papuana* 8—12 (in one flower 7 only). Flowers of the same twig may in the latter species vary in number of stamens. The arrangement is mostly more or less flattened, one anther being found at the ends of the ellipsoid cluster. In several flowers I found occasionally anthers forked towards their apex.

(6) Gynoecium. The shape of the ovary I do not regard as of taxonomic value, being different in different stages of development in bud and during anthesis. In young buds the floral parts are cramped, later they expand a little when the tepals have dropped. In some specimens some ciliae are developed on the terminal blunt edge of the tepals; only in *N. pauciflora* the ovary appears to be distinctly hairy.

(7) Ovary and seed. Contrarily to LAUTERBACH's statement the ovules hang from the top of the cells as rightly observed by GIBBS, GILG & SCHLECHTER, etc. The fruit is a definite drupe turning red to dark blue when ripe. It contains either one (broad ellipsoid) stone or two plano-convex ones. The stony layer produces irregular lamellae towards the interior and the seed appears to be distinctly ruminate.

In the following key I have given the specific characters of the three closely allied species:

Key to the species

1a. Twigs, petioles, underside of the leaves, inflorescence and ovary tomentellous. Inflorescence up to 1½ cm long (mature?). [Bracts 4—4½ by 2½ mm, early caducous. Tepals 2½ mm diam. (in bud?). Stamens ± 8] . . . . 1. **N. pauciflora**

b. Plant subglabrous, not tomentellous; inflorescence sometimes sparsely hairy. Ovary at most with some lines of sparse ciliae. Inflorescence 2—4 cm long. 2

2a. Stamens 6. Bracts not early caducous, thin, 2—2½ by 1 mm. Flowers about 4 mm long. Drupe 10 by 7 mm . . . . 2. **N. arfakensis**

b. Stamens (7—)8—12. Bracts broad, firm, ± orbicular, early caducous, 8—9 mm diam. Flowers about 6—7 mm. Drupe 11—20 by 9—10 mm . . . . 3. **N. papuana**

1. **Nouhuysia pauciflora** (A. C. Sm.) comb. nov. — *Idenburgia pauciflora* A. C. Smith, J. Arn. Arb. 22 : 234. 1941.

N.E.New Guinea. Morobe district, 1400 m, Clemens 3828 (type, not seen).

2. **Nouhuysia arfakensis** (Gibbs) comb. nov. — *Idenburgia arfakensis* Gibbs, Fl. Phyt. Arfak 139. 1917.

N.W.New Guinea. Mt Arfak, Kubree Ridge, 2700 m, Gibbs 6003 (type, not seen,); Mt Arfak, Angi Gita Lake, 1800 m, Kostermans 2217 (B, L), tree 5 m, fls white, fl. fr. Oct. 1948.

3. **Nouhuysia papuana** Lauterbach, Nova Guinea 8^4 : 844. 1912. — *Idenburgia novoguineensis* Gibbs, Fl. Phyt. Arfak 137. 1917. — *Idenburgia pachyphylla* Gilg & Schlechter, Bot. Jahrb. 58 : 246, fig. 2 A—M. 1923. — *Idenburgia elaeocarpoides* Gilg & Schlechter, l.c. 247, fig. 2 N—X; A. C. Smith, J. Arn. Arb. 22 : 233. 1941. — Fig. 2.

Central Celebes. Masamba, near Salu Ranté, 1500 m, bb 24204 (B, L), tree 15 m to 1st branch 6 m, diam. 25 cm; Malili, near Porehoe, 1500 m, bb 19566 (B), tree 15 m, to 1st branch 8 m, 30 cm diam., fl. 15/3/35; ibidem, B. Takale Kadju, 1500 m, bb 24083 (B, L), tree 27 m, to 1st branch 20 m, 21 cm diam., kaju oeé (BareE).

Moluccas. Central Ceram, Makina, 1000—1100 m, Rutten 2240 (B, L), fl. 18/5/19; Eyma 2012 (B).

West New Guinea. Mt Arfak, Kubree Ridge, summit, 2700 m, Gibbs 5654 (L), fl. Dec. 1913, exposed, fastigiate form! (type of I. novoguineensis Gibbs); Mt Arfak, Angi Gita Lake, 1900 m, Kostermans 2198 (B, L), tree 9 m, fl. fr. Oct. 1948; Resi summit, 900 m, G. M. Versteeg 1668 (B, L), fl. white, fr. from green to red to dark blue, fl. fr. 29/8/07 (type of N. papuana Laut.); 9 km E of Habbema Lake, 2740 m, Brass & Versteegh 10472 (L), tree 15 m, 27 cm diam., fl. Oct. 1938; 18 km SW of Bernard camp, Idenburg River, 2150 m, Brass 12661 (L), tree 20 m, fl. fr. 2/39, ovary with some ciliate longitudinal lines; 18 km NE of Habbema Lake, 2200 m, Brass 11078 (L), tree 14 m, fr. Nov. 1938, red; Mt Hellwig, Bijenkorf Bivak, 1750 m, Pulle 681 (B) fl. 14/12/1912, one flower with an oblong segment between stamens and tepals; ibidem, Pulle 647 (B), fr. 18/12/1912, one of the flowers had 7 stamens; Wissel Lake district, 1700 m, Eyma 5177 (B); Mt Cyclops, road from Netar to the coast, 900 m, bb 25014 (B, L), tree 13 m, 30 cm diam., fl. 26/6/38.

East New Guinea. Hunsteinspitze, ca 1300 m, Ledermann 10940 (B), Ledermann 11324 (B), (types of Idenburgia elaeocarpoides Gilg & Schlechter); Schraderberg, 2070 m, Ledermann 11883, 12075 (B), with young inflorescence showing bracts not described (type of Idenburgia pachyphylla Gilg & Schlechter); Boridi, C. E. Carr 13149 (L), fr. 14/9/36, tree 30 m; ibidem 1500 m, Carr 13148 (L), fl. 14/9/35; ibidem 1500 m, Carr 13240 (L), tree 27 m, fl. 18/9/35; Lala River, C. E. Carr 14056 (L), tree 15 m, fr. 27/12/36; ibidem, 1650 m, Carr 14055 (L). Morobe district, Yunzaing, 1350 m, Clemens 3978; Ogeramnang, 1800 m, Clemens 5122.

ON THE SUBMICROSCOPIC STRUCTURE OF CUTICULAR CELL WALLS

BY

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With plates I—IV

INTRODUCTION

Mainly as a result of studies on double refraction before and after extraction of waxes, Miss M. MEYER (1938) concluded that the cuticular layers of leaves from *Clivia nobilis*, *Gasteria*, *Dasylirion* and *Yucca* consisted of two layers, i.e. an outer layer with cutin and wax and an inner layer containing in addition cellulose and pectin.

The double refraction of the outer layer was always negative with reference to the cuticular surface; the highest refractive index was radial. However, after extraction of waxes with boiling [1] pyridine for 120 hours or after melting them at 100° C, this layer became isotropic provided the section was mounted in benzene ($n = 1.50$) to eliminate the form double refraction of the pores in the cutin skeleton structure (Gerüstsubstanz). This proved that the original double refraction was due to extractable wax molecules.

Since a solution of friedelin (from cork wax) in *m*-cresol showed positive streaming double refraction, it was assumed that the cutin wax molecules would behave similarly [2]. Accordingly the negative birefringence of the outer cuticular layer could only be explained by assuming a radial orientation of these molecules. Presumably the wax molecules are crystallized in tangentially oriented platelets, since a positive rodlet form double refraction was discernable when extracted sections were mounted in liquids with refractive indexes higher or lower than 1.50. It was assumed, but in our opinion not proven, that these platelets were equidimensional in surface view.

The inner parts of the cuticular layers of the plants mentioned, differed in one respect from the outer parts: they contained in addition cellulose and pectin. In *Dasylirion* the double refraction of the tangentially oriented cellulose predominated and produced positive birefringence (with reference to the leaf surface). In *Yucca* it just compensated the wax birefringence, thereby producing isotropism. In *Gasteria* and *Clivia* the wax birefringence predominated. Positive double refraction appeared after extraction of the waxes in *Gasteria*, whereas *Clivia* is said to become isotropic, since the cellulose double refraction was too faint to be discerned. That cellulose was actually present in *Clivia* was deduced from the yellow-violet dichroism of sections coloured with chlor-zinc iodide after having been treated with hot concentrated alkali.

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[1] In MEYERS' article no reference as to the temperature of extraction was made, but Prof. A. FREY-WYSSLING privately informed the author, that the extractions were performed at the boiling point.

[2] WEBER (1942) has shown, that the streaming double refraction of wax solutions may be positive or negative, dependent on the orientation of the molecules in anisotropic molecular aggregates which are usually present in solutions at normal temperature. Strictly speaking therefore, the observations of positive flow birefringence of a wax solution did not fully permit MEYER to conclude that wax molecules are positively birefringent. However, the long aliphatic chains of most plant waxes, with little or no polar side groups certainly exclude negative molecular birefringence.

This picture of the submicroscopic structure of cuticular layers seemed to be well founded and it was tacitly assumed to be representative for all plant cuticles. However, the author (1951) observed that the cellulose-free cuticles of *Tradescantia* staminal hairs did not become isotropic after extraction for several hours in boiling chloroform and in boiling pyridine, although they were mounted in liquids matching the refractive index of the cutin very closely. If the double refraction had been due to normal waxes, freely soluble in solvents, then these would have been extracted very rapidly from the very thin cuticles. Hence, the residual double refraction was not due to normal waxes. It could only be explained by assuming the presence of radially oriented (probably wax-like) molecules, which were chemically bound in this position.

The object of our investigation was to find out whether or not the presence of such chemically bound radially oriented molecules had also to be assumed in the cuticular layers studied by MEYER. The faint residual double refraction from which their presence was deduced in the case of *Tradescantia*, might have been overlooked because she did not mention any special precautions taken to detect such effects. In our study of *Tradescantia* cuticles we had to use the extremely sensitive method of LAVES and ERNST (1943) in order to detect this low intrinsic double refraction and identify its character.

Contrary to MEYERS' findings the cuticles stayed negatively birefringent after prolonged extraction and after impregnation with benzene or other liquids with similar refractive index. The next question was whether this could be ascribed to cellulose or not. This entailed the isolation of the cellulose "skeletons" of the cuticular layers of *Clivia* in order to study their optical properties. The sequence of these investigations will be reversed in their discussion; the latter point will be treated first.

§ 1. SUBMICROSCOPIC STRUCTURE OF THE CELLULOSE IN THE CUTICULAR MEMBRANE OF *Clivia nobilis*

By "cuticular membrane" we mean all the cutinized parts of the cell wall, comprising the cuticle *sensu stricto* and the cuticular layers. As first described by ANDERSON (1928), the cutinized layers are separated by a pectin layer from the inner cellulose layer which lines the lumen of the epidermal cell.

We were therefore able to obtain our cuticular membranes free from the pectin and cellulose layers, by dissolving the pectin. This was done by keeping isolated pieces of leaf in 5 % H_2O_2 at 50° C for a few days (KISSERS' maceration method), or by boiling for half an hour in 5 % Na_2CO_3 or for several hours in 2 % ammonium oxalate. The leaf tissue is thereby macerated and, provided the leaf edges have been taken off beforehand, the separate membranes of the upper and the lower leaf surfaces can be collected. Those of the lower side usually showed many more stomata and less elongated cells. As a rule many highly birefringent cellulose walls of epidermal cells still adhered to the membranes, especially to those from the upper leaf surface. The adhering cellulose may be rubbed off with a brush, but is more easily removed by a short immersion in cuprammonium (SCHWEITZERS' reagent), followed by consecutive washes in concentrated ammonia, acid and water [1].

Fig. 1a represents a surface view of a cuticular membrane from the upper surface of the leaf. The original epidermal cell boundaries are marked by stiff cuticular ridges, which projected into the walls separating the cells. This is more clearly visible in transverse sections as in fig. 1b.

First we tried to dissolve the cutin out of these cuticular membranes by using the same methods MEYER already tried without success, viz. a prolonged immersion in a saturated solution of ClO_2 in 50 % acetic acid and heating in 17 % NaOH at 100° C for 1 — 3 hrs. However, too much cutin remained and no cellulose reaction was seen with chlor-zinc iodide.

Then we tried a high temperature alkali treatment as is applied in the soda process of the wood pulp industry. Best results were obtained by putting pieces of membrane in tubes with 4 % NaOH and heating these for ½ — 1 hr in an oil bath of 160° C. Since fused glass tubes sometimes exploded and always corroded, we used small tin-plated steel tubes, tightly closed with a screw and an annealed red copper gasket. After cooling, the contents were centrifuged and consecutively washed in alcohol and water. The remaining cellulose skeletons coloured red-brown with chlor-zinc iodide, but a blue colour was obtained after repeated bleaching with sodium hypochlorite (0.7 % act. Cl) and hot 3 % $NaHSO_3$.

However, they were unsuitable for studying the cellulose orientation because the cells appeared to have shrunk considerably. Shrinkage also occurred on applying the hot glycerol method of VAN WISSELINGH (1898). We tried temperatures between 210 and 300° C for ½ — 6 hrs.

This shrinkage did not occur on heating in alcoholic alkali (12 g KOH in 12 ml. water made up with 96 % alcohol to 100 ml.), a well-known reagent for solution of cutin. More than 5 hrs of boiling with reflux (95° C) was needed to remove the cutin completely, whereas in steel tubes at 160° C half an hour was sufficient.

The dissolved cutin could be eliminated completely by centrifugation of the tube contents while still hot and by consecutive washing in hot alcoholic alkali, alcohol and water.

---

[1] One need not fear a solution of the cellulose from the cuticular membrane. We obtained cellulose skeletons of membranes, which had been kept in cuprammonium for many hours.

The iodine dichroism (fig. 2) and the double refraction of Congo red coloured specimens suggest a fibril orientation as indicated in fig. 3a.

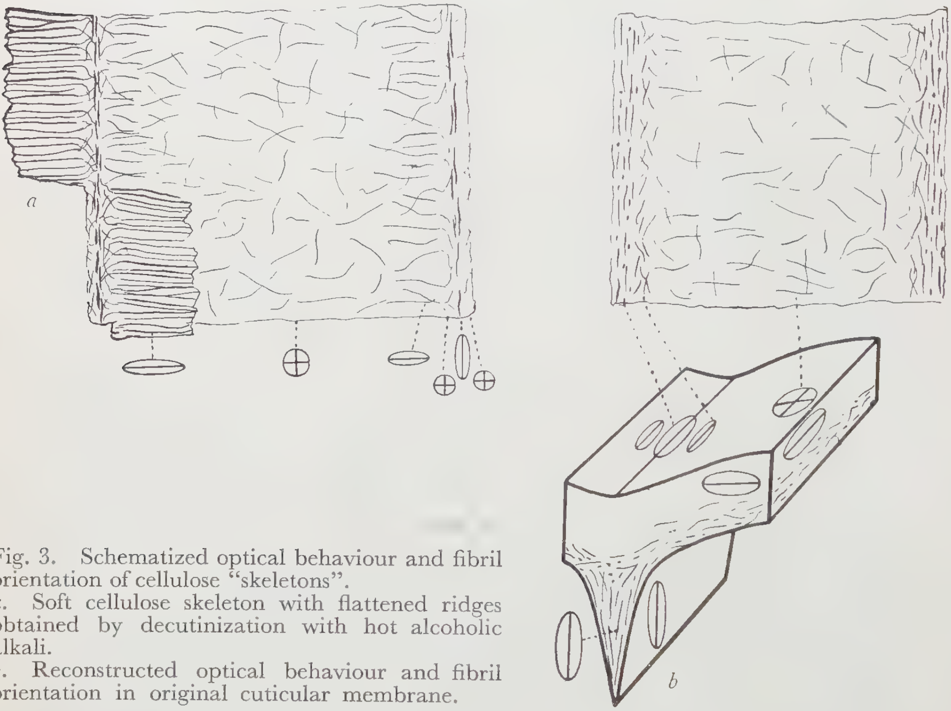

Fig. 3. Schematized optical behaviour and fibril orientation of cellulose "skeletons".
a. Soft cellulose skeleton with flattened ridges obtained by decutinization with hot alcoholic alkali.
b. Reconstructed optical behaviour and fibril orientation in original cuticular membrane.

Most conspicuous are the ridges. The cellulose fibrils in them show a high degree of orientation in radial direction. They are usually flattened on the slide, demonstrating their loss of rigidness on decutinization. Where the ridges are attached to the tangential part of the membrane, i.e. on the cell boundaries, a thin strip with axial orientation is present. This is bordered by two narrow isotropic strips and two somewhat broader zones with predominant transverse cellulose orientation. The central parts of the "cells" are isotropic both in long and in short cells.

This applies to the cellulose skeleton as it is lying flat on the slide, but in the cutinized original membrane it will be somewhat curved near the ridges (fig. 1b). As a result, on surface view, the situation near the ridges will be changed. A probable reconstruction of the optical behaviour as far as the cellulose skeleton is concerned, is depicted in fig. 3b. In accordance with Meyers' suggestion (l.c. p. 567) the cellulose is supposed to be mainly located in the inner parts of the membrane. However, additional proof of this seems desirable.

§ 2. Optical behaviour of cuticular membranes of *Clivia nobilis*

a. Non-extracted membranes

M. Meyer studied both sections and isolated cuticular membranes. The optical properties she described were presented schematically as in fig. 4a.

We were not able to corroborate certain details of this picture as will become apparent on studying fig. 4b and c.

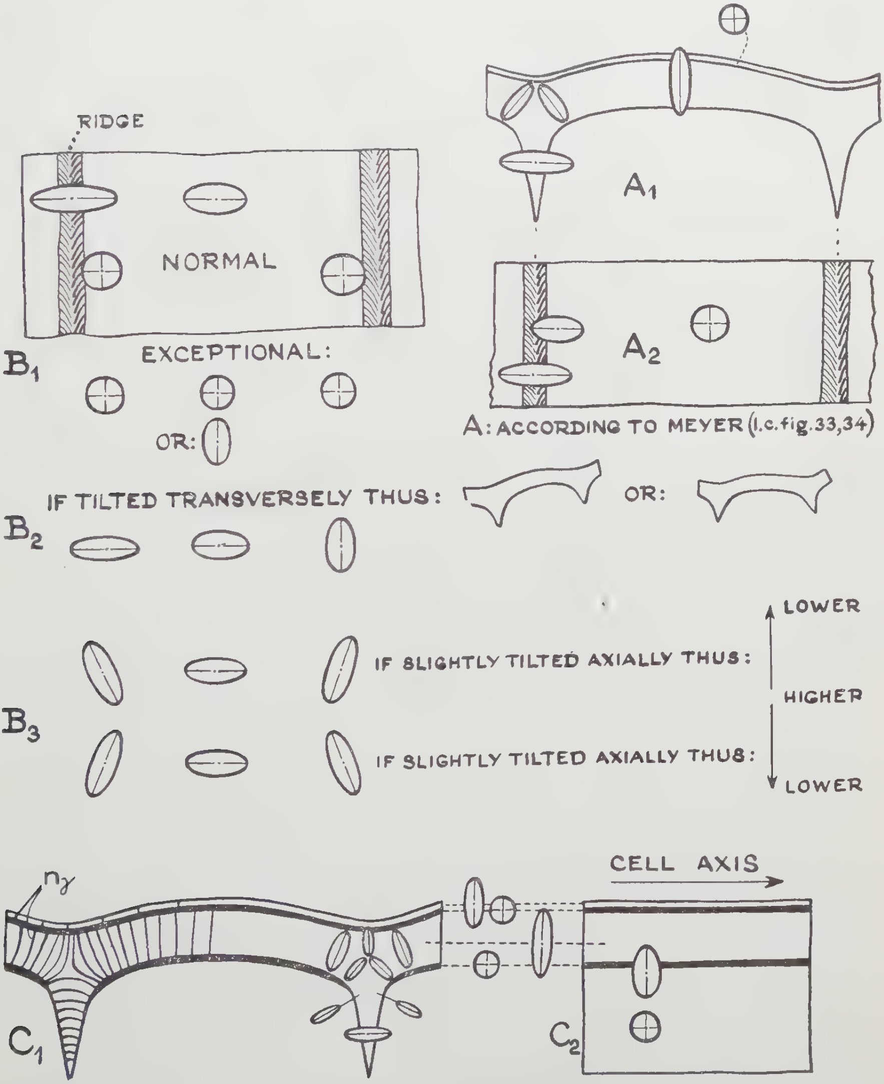
RIDGE
NORMAL
A1
A2
A: ACCORDING TO MEYER (l.c. fig. 33,34)
B1
EXCEPTIONAL:
OR:
IF TILTED TRANSVERSELY THUS:
OR:
B2
B3
IF SLIGHTLY TILTED AXIALLY THUS:
IF SLIGHTLY TILTED AXIALLY THUS:
LOWER
HIGHER
LOWER
CELL AXIS
nγ
C1
C2

Fig. 4. Double refraction of cuticular membrane of *Clivia nobilis*. *a.* According to Meyer; a_1 transverse section and a_2 surface view. b_1 normal surface view, $b_{2,3}$ view with membrane tilted as indicated. c_1 transverse and c_2 axial section.

Firstly, the central part of the "cells" observed radially (surface view), were usually negatively doubly refractive with respect to the cell axis and not isotropic. The retardation, as measured with a Leitz elliptic compensator ($^1/_{10}$ λ plate) was at most 10 mμ with membranes from the upper leaf surface, and lower in membranes from the lower leaf surface. Near the cell boundaries isotropic zones were as a rule visible (fig. 4b$_1$). The photomicrograph of fig. 5 demonstrates this. Admittedly, one sometimes observes membranes behaving differently, as is also depicted in fig. 4b$_1$.

If the membrane on the spot studied is not lying flat but is slightly tilted, as often occurs even when covered with a thick coverslip, one observes a different behaviour of the two sides of the same cell. If the membrane is inclined in an axial direction (with a transverse axis) as indicated in fig. 4b$_3$, the explanation is obvious when the direction of the nγ lines adjacent to the ridges, as drawn in fig. 4c$_1$, is taken into consideration. If the membrane is inclined in a transverse direction, as depicted in fig. 4b$_2$, the behaviour of the left-hand part of the cell drawn is also obvious, but not the behaviour of the right-hand part. This will be considered in section 3.

Furthermore, the double refraction of transverse and axial sections of the membrane, differs in details from the picture MEYER gave, as a comparison of fig. 4a$_1$ with fig. 4c$_1$ will show. Firstly, the cuticle *sensu stricto* is not isotropic in sections as she and all previous investigators claimed, but faintly negative with respect to the leaf surface (nγ radial). This is clearly visible in very thin (3 μ) sections only, such as in the photomicrograph of fig. 6. Between this cuticle and the strongly negative (± 30 mμ in 3 μ sections) cuticular layer an isotropic line occurs, which was also not described earlier [1].

As FREY (1926) has already described, the central part of the cuticular layer is the most brightly birefringent one. There is a gradual reduction to isotropism or even faint positive double refraction in the innermost thin layer. This is not composed of pectin only, for non-cutinized pectin and cellulose had been previously dissolved by H_2O_2 and cuprammonium. The inner layer in question readily stained with Sudan III reagent and therefore belongs to the cuticular layer.

Fig. 4c$_1$ also presents a more detailed picture than MEYER gave of the orientation of nγ in and above the ridges and adjacent to them. The nγ lines are always perpendicular to the nearest cuticular surface. Fig. 4c$_2$ depicts the isotropism of axial ridges as seen in axial sections (surface view of the flat side of the ridge).

We notice that the optical properties outlined here are quite unaffected by the refractive indices of the mounting liquids, which proves that form double refraction in non-extracted membranes is nullified by the high intrinsic double refraction of waxes. Our studies of the cellulose skeleton (section 1) allow us to conclude that the cellulose double refraction is also much too faint to change the final result.

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[1] Thin sections were put at our disposal by our collaborator: G. SCHOLTEN.

b. Residual double refraction in extracted membranes

As stated in the Introduction, MEYER extracted sections of *Clivia* epidermal cells up to 120 hours with boiling wax solvents, particularly pyridine, and then observed isotropism in the cuticular layers, provided they had been mounted in benzene (n = 1.50). The double refraction of non-extracted sections also disappeared (reversibly) on heating at 100° C. After heating at 210—230° C double refraction did not reappear on cooling. The obvious conclusion was that the double refraction was wholly due to oriented wax crystals, which could be extracted with fat solvents, could be melted at 100° C and were definitely destroyed at about 220° C. Apparently the cellulose double refraction was negligible.

We have already pointed out why a repetition of these experiments was deemed desirable. In addition to cuticular membranes, isolated as described earlier, we used microtome sections of 20 μ thickness from fresh leaves, both old and young. They were dehydrated with absolute alcohol prior to extraction. After extraction or heating, the membranes or the sections were mounted in benzene or in methylbenzoate (n = 1.512) and studied between crossed nicols using a strong light source and applying the method of LAVES and ERNST (l.c.) or by using a sensitive Leitz elliptic compensator provided with a 0.1 λ plate.

Having observed that extraction with chloroform, pyridine or CCl_4 at room temperature up to 16 days, at 50° C up to 10 days, or at the boiling point for 1 day visibly reduced but by no means destroyed the double refraction of the cuticular membrane, we increased the extraction period to 8 days with boiling chloroform or to 6 days with boiling pyridine, both followed by a 5 day extraction with boiling CCl_4. Especially during extraction with pyridine the membranes and sections blackened somewhat and thus masked the double refraction. We therefore usually bleached them in Ca-hypochlorite and $NaHSO_3$ solutions prior to dehydrating with absolute alcohol and mounting in benzene. Occasionally some sections out of each batch were studied for absence of birefringence. A faint negative double refraction persisted in the sections of all samples. Since no changes were detectable during the last few days of the respective extraction periods, we saw no point in prolonging the treatment.

Since the cuticular membrane is about 5 μ thick and is sectioned at 20 μ distances, all free wax molecules may be supposed to have dissolved during such very long extraction periods, especially since pyridine boils above the wax melting point. In our opinion the extraction time was already long enough to involve the possibility of chemical changes, notably at the high boiling point of pyridine (115° C).

Fig. 7a and b clearly demonstrate this residual negative double refraction of the cuticular layer in a thick transverse section. The retardation in transverse sections of 20 μ usually varied between 30 and 45 mμ, as against 7—30 mμ in axial sections. The ridges in sections did not become negatively birefringent (with reference to the leaf surface) as the radial cellulose orientation lead one to expect, but stayed positively birefringent, just like those which were not extracted.

In thin (6 μ) axial and transverse sections of extracted membranes, observed with high magnification (fig. 7c), three layers could be discerned in the cuticular membrane, viz. a thin one on the outer and on the inner sides and a thick central layer. The two thin layers were faintly positive (± 4.5 mμ in 6 μ transverse sections); the central part was distinctly negative (± 7 mμ) and apparently outweighed the influence of the two thin layers when a lower magnification was used. The cut ridges also, whether axial or transverse, showed three layers. At first we considered this three layer structure to be a demonstration of progressive extraction from the outside inwards, but the image did not change on further extraction. Hence we may assume this to be caused by differences in structural or chemical properties. The outer thin layer obviously conforms to the cuticle *sensu stricto*, already distinguishable in non-extracted sections (fig. 6) and the inner thin layer might be that part of the cuticular layer which contains relatively much cellulose and a small quantity of cutin and wax.

In a radial view of extracted cuticular membranes mounted in benzene or methylbenzoate, the tangential parts are usually isotropic, sometimes faintly positive or negative (fig. 8). In the middle of the cell boundaries there is a thin negatively birefringent strip, obviously due to the ridge (fig. 7c). This is bordered by two isotropic strips and two broader zones with positive double refraction.

When observed with low magnification the central negative part in the axial ridges was dominated by the two outer positive ones, whereas in the transverse ridges usually the central part predominated.

Having observed a residual negative double refraction in extracted sections, we subsequently tried to see whether this also occurred when sections were heated to temperatures of 220—240° C, a procedure said to cause irreversible disappearance of all double refraction. Extracted and non-extracted sections were put into a small glass tube and this was kept in a sand bath at 220—240° C for 15 min. Alternatively, sections lying under a thick cover glass on a slide were held between a pair of forceps in the hot sand. After cooling, benzene was applied under the coverslip. Even without bleaching a similar faint negative double refraction was visible as was seen with extracted specimens.

c. *Form double refraction in extracted membranes*

In confirmation of Meyers' observations we observed a form double refraction in the cuticular layers of sections and in membranes which previously had been extracted, bleached and dehydrated as described earlier.

Thick (25 μ) transverse and axial sections or the membranes were mounted in absolute alcohol and then retardation at certain selected points was measured with the elliptic compensator, using white light. Then, without touching the coverglass, the preparation was

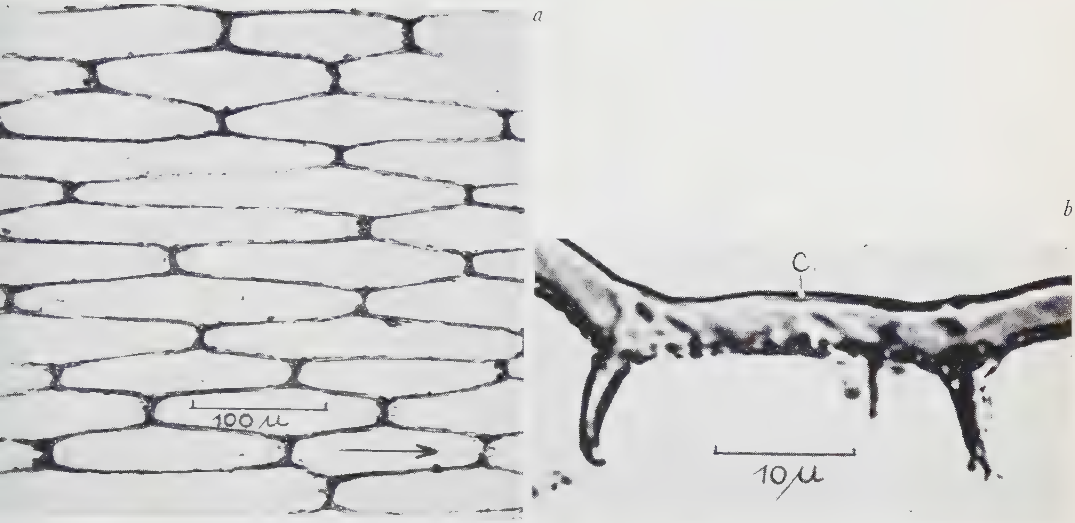

Fig. 1. *a.* Surface view of cuticular membrane of upper leaf surface of *Clivia nobilis*; leaf axis indicated.

b. Transverse section through a similar membrane, coloured with malachite green. Note cuticle *sensu stricto* (c) and more strongly coloured inner layer.

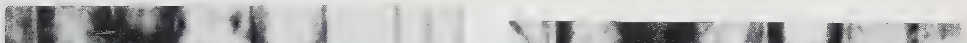

Fig. 2. Cellulose "skeletons" of cuticular membranes coloured with chlor-zinc iodide and photographed in polarized light. Vibration plane of polarizer indicated. Note the soft flattened "ridge skeletons" and the index ellipses indicating fibril orientation.

PLATE II

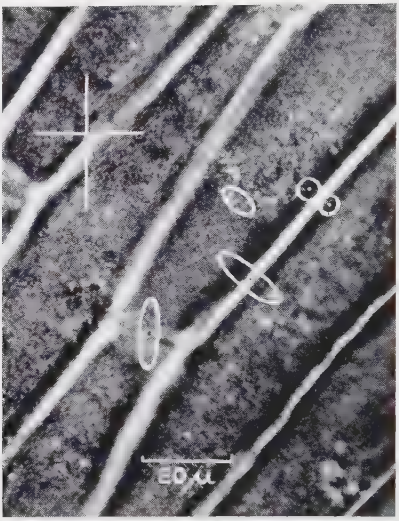

Fig. 5. Radial view of cuticular membrane between crossed nicols. Vibration planes and index ellipses indicated.

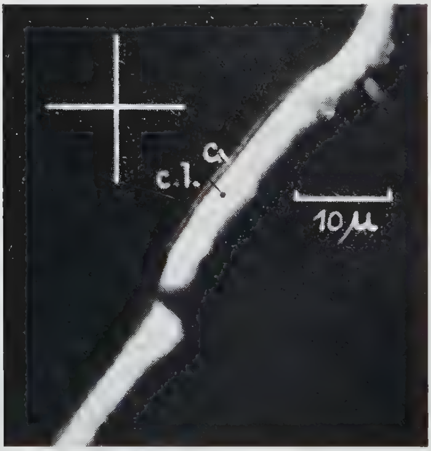

Fig. 6. Thin transverse section (3 μ) through non extracted cuticular membrane, seen between crossed nicols. Note the doubly refractive cuticle (c) and the isotropic zone between cuticle and cuticular layer (c.l.).

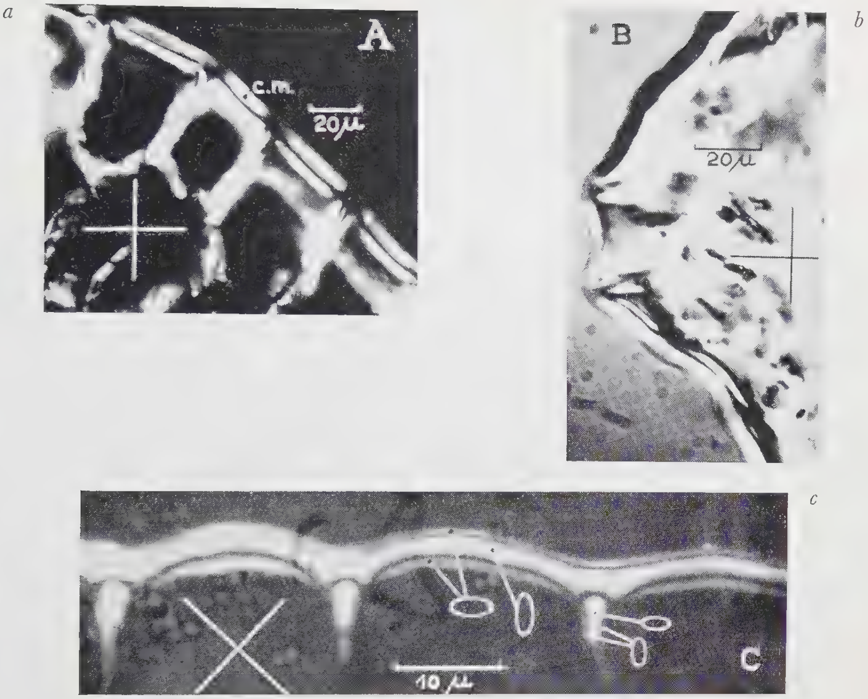

Fig. 7. Transverse sections of extracted cuticular membranes mounted in benzene and observed between crossed nicols.

a. Thick transverse section observed with low magnification, showing conspicuous negative residual double refraction in cuticular membrane (c.m.).

b. Similar section with compensated double refraction in the cuticular membrane of the upper part.

c. Thin section observed with high magnification showing three layers with different optical properties (indicated by ellipses).

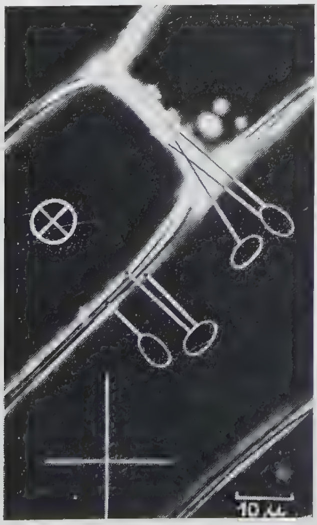

Fig. 8. Radial view of extracted cuticular membrane between crossed nicols. Vibration planes and direction of nγ indicated.

PLATE IV

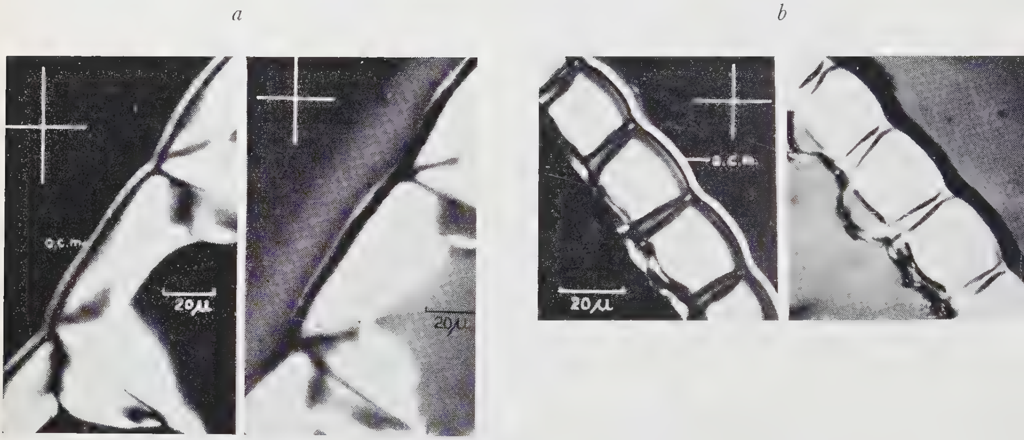

Fig. 12. On the left: extracted sections of cuticular membranes between crossed nicols. On the right the same spot compensated for the negative double refraction of the outer layer (o.c.m.).
a. *Gasteria trigona.*
b. *Dasylirion serratifolium.*

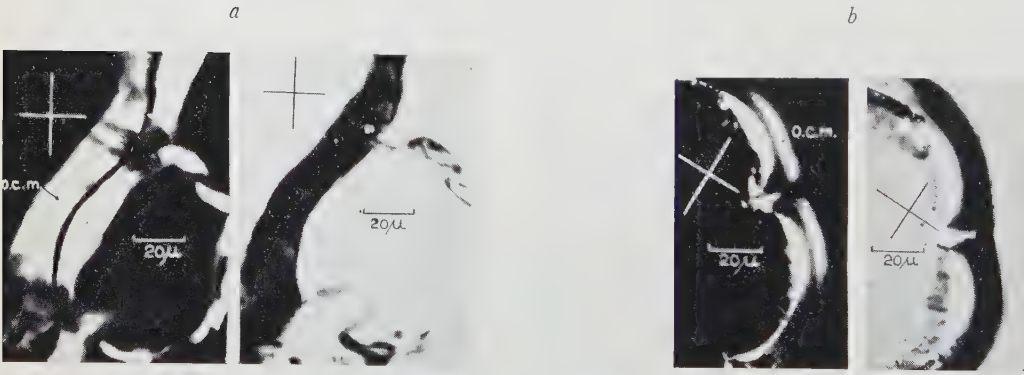

Fig. 13. On the left: extracted sections of cuticular membranes between crossed nicols. On the right: the same spot compensated for the negative double refraction of the outer layer (o.c.m.).
a. *Yucca aloifolia.*
b. *Aloe glauca.*

dried at 50° C for several hours. Then benzene was applied under the coverglass and the retardation was determined again at the same points. At first we thought that it would take some time to attain complete penetration of the mounting liquid, but the retardation almost immediately attained its final value. This is understandable since cutin is lipophilic as are the liquids themselves. Finally the retardation was measured after impregnation with CS_2. The same procedure was followed with 6 μ sections obtained from paraffin-embedded extracted membranes. In such sections the three layers as depicted in fig. 7c were studied separately.

The results are given in table 1.

TABLE 1

Form double refraction and intrinsic double refraction (benzene) of extracted cuticular membranes

Imbibition liquid	nD	Average retardation in mμ of cuticular membrane in: 25 μ sections		layers of 6 μ section		Surface view of central part of "cell"	Character of predominant double refr. in radial view of ridges:	
		axial	transverse	outer	middle		axial	transverse
Abs. alcohol	1.363	+10	+(0.8?)	+14.3	4.5	—2.5	+	+
Benzene	1.500	—19	—48	+ 4.5	—7.0	+1.7	+(0.—)	—(0.+)
CS_2	1.623	—11	—42	+ 7.3	—5.1	+	+(0.—)	—, 0, +
		+ or — with resp. to leaf surface				+ or — referring to cell axis	+ or — referring to ridge direction	

If we disregard the intrinsic double refraction, seen when mounted in benzene and only consider the character and the magnitude of the changes induced by mounting in alcohol or CS_2, we are studying the WIENER form double refraction effect. Apparently there is a WIENER effect in all cases, viz. in axial and transverse sections, in the layers of the sections, on surface view of the central parts and in the ridges. This proves that there are non-equidimensional pores everywhere in the cutin structure. The orientation of the major pore dimension may be deduced from the index ellipsoid of the form double refraction.

In axial as well as in transverse sections the higher index is tangential and the shorter one (nα) radial. Hence the shortest pore dimension must be the radial one. Because the WIENER effect is greater in transverse than in axial sections of equal thickness the pores (or the projection of the pores) must be longer in a transverse than in an axial direction. This is confirmed by the character of the WIENER effect in radial view, which allows one to conclude that nγ of the index ellipsoid of form double refraction is transverse and nβ axial. This leaves two possibilities: either the pores are tangentially oriented oblong platelets with their longest dimension transverse, or they are tangentially oriented rodlets having a predominantly transverse orientation.

In the ridges the minor pore dimension must be oriented perpendicular to the surface of the ridge. Bearing in mind the cellulose orientation in the ridge, it seems very probable that the major pore dimension will be oriented radially like the cellulose. The form double refraction of axial ridges, sometimes visible in axial sections, might have confirmed this. However, it was impossible to make reliable observations on such ridges, since they were rarely lying flat and since they were practically isotropic.

As we have seen, MEYERS' results were markedly different. At first sight one feels inclined to ascribe the alleged absence of residual intrinsic double refraction in extracted sections to a mere oversight, due to the use of less sensitive methods or to an omission of bleaching of the darkened extracted sections. Then, however, she should not have detected the WIENER effect, unless it was much more conspicuous in her objects than in ours. This does not apply since the retardation difference measured by her in 10 μ axial sections with alcohol and benzene as mounting liquids, was 8° with the Sénarmont $\frac{1}{4}$ λ compensator or 24.5 mμ, as against 29 mμ retardation difference in our axial sections of 20 μ thickness. Apparently the methods she used were sensitive enough.

Then one might suppose that in her sections the two outer, positively birefringent layers as seen in fig. 7c were more pronounced and the central layer less, resulting in apparent isotropism when studied with low magnification. However, the fact that in the other plants, mentioned in section 4, a similar divergence of results is seen, does not make this possibility very likely.

It might be that in her objects for some unknown reason the waxes were more fully extracted and were more heat-sensitive than in ours. Since this should apply to all plant species examined, this seems unlikely too.

§ 3. PROPOSED CONCEPTION OF SUBMICROSCOPIC STRUCTURE OF CUTICULAR MEMBRANE OF *Clivia nobilis*.

Our experimental results may be summarized as follows.

The orientation of the cellulose fibrils, probably occurring mainly in the inner parts of the cuticular layer, has been depicted in fig. 3. The effect of the cellulose on the optical properties is indicated in fig. 9 with the ellipses marked C.

The predominant orientation of the wax molecules must be parallel to the nγ lines as drawn in fig. 4c$_1$. The effect on the optical properties is indicated in fig. 9 by the ellipses marked W. There are either more or better oriented wax molecules in the central part of the cuticular membrane than in the cuticle *sensu stricto* and in the innermost layer. The wax must be crystalline since the double refraction nearly disappears on heating. These crystals must be located in pores.

The study of the form double refraction (ellipses marked F in fig. 9) indicated two possibilities as to the pore-shape in the tangential parts of the cuticular membrane, viz. either tangentially oriented oblong platelets with their longest axis transverse, or tangentially oriented rodlets also predominantly oriented in a transverse direction. However, in the latter case it would be inexplainable why the wax molecules are mainly oriented radially. They might as well be oriented in other directions perpendicular to the rod-axis. If we assume oblong platelets and take account of the tendency of waxes to crystallize in platelets (KREGER 1948, WEBER 1942), then radial orientation is self-evident.

We may imagine the wax-filled pores as being shaped like submicroscopic rulers, which are oriented with their flat sides perpendicular to the nγ lines drawn in fig. 4c$_1$ and with their longest dimension predominantly transverse to the cell axis. This concept is presented in fig. 9. In reality, of course, the pores will not be like rulers, but will have very irregular shapes, being moreover connected with each other and thus constituting an anisotropic porous structure as in a stretched rubber sponge.

As indicated in section 2c, we cannot be as definite in describing the pore structure in the ridges. There must be platelets here too and the shortest dimensions must be located as drawn in fig. 9, but we do not know whether they are oblong or not or how the oblong platelets are oriented. Our hypothesis favours a radial orientation of the longest dimension.

There are some other phenomena, described in previous sections, which we shall have to explain in order to arrive at a tentative idea of the submicroscopic structure, which tallies with all facts known.

Viewed in a radial direction, non extracted membranes are negatively doubly refractive with reference to the cell axis; (see index

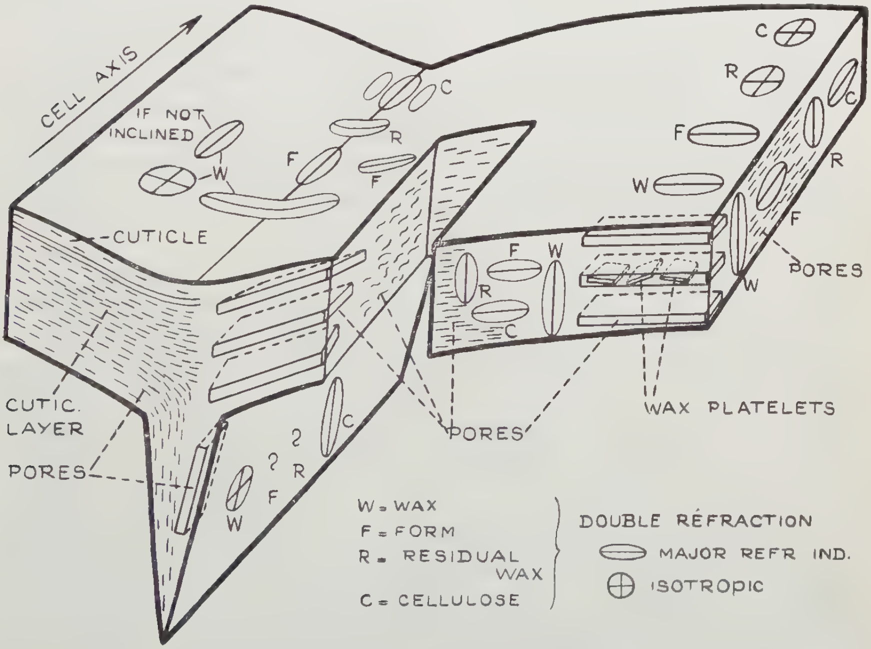

Fig. 9. Tentative schematical representation of submicroscopic structures in *Clivia nobilis* cuticular membrane. Index ellipses of the components contributing to the double refraction are indicated in transverse and axial section and in surface view.

ellipses marked W in fig. 9). This cannot be due to cellulose double refraction, because the cellulose skeleton is isotropic when observed in a radial direction (fig. 3). Neither can it be due to form double refraction because it does not disappear when the membrane is mounted in benzene. It must therefore be due to a special orientation of wax molecules. It is self-evident that not all of these will be oriented strictly radially. Many will deviate slightly from this position, inclining to one direction or another. Such an inclined molecule (or group of molecules: crystals) will produce some double refraction of its own when the membrane is viewed in a strictly radial direction. The negative double refraction in question shows that molecules inclined to the transverse direction are more numerous than those inclined to the axial direction, or the inclinations are more pronounced or both.

Thus far there is little theory in this. But how is this phenomenon to be explained? As we saw, the pores may be imagined as transversely oriented rulers. It seems obvious that these rulers will tend to incline in axial direction (as depicted with the three "rulers" near the ridge in fig. 9) rather than in transverse direction. If the pores would each contain one big wax crystal filling up the whole pore space, then the preference for axial inclination would produce positive double refraction whereas a negative double refraction is observed. However, it is rather unlikely that the pores, which in reallity of course have a very irregular shape, will each contain one big wax crystal. They will be filled with aggregates of many small crystalline wax platelets, also irregularly shaped, but for the sake of convenience to be regarded as square platelets. If these crystallites are not too small compared with the pore space, they will more readily incline along the length of the oblong pore space than across its breadth. This state of affairs is demonstrated in fig. 10 [1], which of course is entirely theoretical, merely illustrating the effect in question. Although admittedly, this picture is rather hypothetical, as far as we can see it is the most likely explanation, which fits all the known facts.

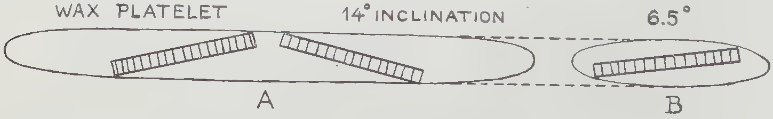

Fig. 10. Demonstration of effect of greatest pore dimension on predominant direction of inclination of wax platelets located in it. *a.* lengthwise; *b.* breadthwise section through same hypothetical pore space.

Of course the inclination of the wax crystals will also be affected by the inclination of the pore spaces themselves. Probably this effect comes into play in the isotropic zones adjacent to the cell boundaries, which are visible when wax-containing membranes are viewed in a radial direction between crossed nicols (fig. 5). Because in these areas the membrane is somewhat curved, the nγ lines are also inclined (fig. 4c$_1$). This should merely increase the already negative double refraction. Instead, the double refraction disappears. If the membrane is tilted in a transverse direction so that the membrane in one of the two curved isotropic cell parts is now strictly perpendicular to the direction of view this part becomes positively doubly refractive (fig. 4b$_2$). What is the explanation of this?

---

[1] The wax molecules are drawn perpendicular to the crystal surface since natural waxes crystallize mostly in the rhombic form (Kreger, 1948). In fatty acids and soaps the molecules are often obliquely oriented.

First we thought that the double refraction of the cellulose skeleton as depicted in fig. 3b could explain it. Such an explanation was given by MEYER (l.c. pag. 582) for the occurrence of similar positively birefringent zones in surface view of non-extracted membranes of *Gasteria*. We have no reason to reject her explanation, but it does not apply to the problem in question with *Clivia*.

Firstly the cellulose double refraction as seen in the cellulose skeletons is much lower than the positive double refraction seen in the upper parts of the slightly tilted membranes. Moreover the cellulose can only produce positive double refraction in the highly curved parts at the base of the ridges (fig. 3b), for if the cellulose skeleton is lying flat as in fig. 3a, the double refraction near the ridges is negative.

Secondly, if the wax is extracted, the isotropic zones in question do not become broader and do not change into positive zones, as would be expected. Admittedly, small positive zones are produced, which are very probably due to cellulose double refraction (fig. 8), but these are less broad than the isotropic zones in the wax-containing membranes (compare fig. 5) and are too faint.

Hence we must assume that near the cell boundaries the predominant inclinations of the wax molecules are axial instead of transverse as in the central parts. It is only owing to the fact that the membrane is somewhat curved and therefore observed in a slightly inclined position that isotropism occurs. By eliminating the inclination, positive double refraction appears, as indicated in fig. 4b$_2$, right part.

What might be the reason for the predominant axial inclination in these zones? The character of the form double refraction (see F ellipses in fig. 9) excludes the presence of axially elongated or equidimensional pores. We can see only one more possibility, viz. that the inclinations of the "ruler-like" pores themselves are more marked here than in the central part. This is depicted schematically in fig. 9. In reality of course there are no ruler-like pores; it is better to say that the pore-space is less flattened tangentially, but more irregular than in the central cell parts.

RESIDUAL INTRINSIC DOUBLE REFRACTION. It has been shown in section 2b, that extracted or heated sections and membranes show a residual negative double refraction when mounted in benzene to eliminate form double refraction. As depicted in fig. 7c there are three layers, differing in character, but the middle layer predominates. The resulting effect is indicated in fig. 9 by the ellipses marked R.

It cannot be due to the only crystalline substance already known to occur in extracted membranes, viz. cellulose. Therefore we must assume the presence of another non-extractable and non-melting substance as we already postulated for the cuticles for *Tradescantia* staminal hairs (1951).

We know nothing of the character of this substance. Maybe the cutin skeleton, which consist of polymerised dicarboxylic and hydroxycarboxylic acids, is slightly doubly refractive. We prefer, however, to propose the hypothesis that some of the wax molecules, perhaps chemically different from the bulk of this material, are chemically bound in an oriented position to the cutin walls of the pore space. Not to the cellulose because the residual double refraction also occurs in the outer, allegedly cellulose-free, part of the cuticular layer of *Clivia* (as well as of other plants: see section 4).

These might for instance be long-chain aliphatic alcohols or fatty acids, bound with their polar group to the carboxyl or hydroxyl groups in the cutin and oriented with their aliphatic chain perpendicular to the pore surface. We thus imagine the pores lined with a monomolecular layer of bound wax molecules protruding into the empty pore space, originally filled with extractable, melting, crystalline waxes.

If the pore shape is taken into consideration, this assumption will also explain why the residual double refraction is more conspicuous in transverse than in axial sections. This cannot be due to the cellulose. If we once more imagine the pores as transversely oriented ruler-shaped structures, fig. 11 immediately demonstrates that in transverse sections the preponderance of radially oriented molecules must be greater than in axial sections. The residual double refraction of the central part of the ridge may be explained in the same way.

In surface view of extracted membranes mounted in benzene one should expect positive double refraction. As stated in section 2b however, isotropism is found and sometimes a very faint positive or negative double refraction. It might be that in fact there is a faint residual positive double refraction, but usually compensated by equally small form double refraction. One cannot expect the form double refraction to disappear completely on the boundary cutin-wax-benzene; moreover there will always remain local refractive index differences between cutin and benzene, since probably the density of the cutin will vary locally.

As can be seen in table 1, there is form double refraction in each of

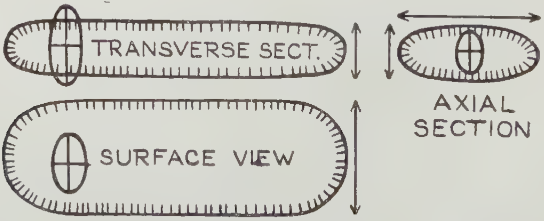

Fig. 11. Schematic representation of different sections of a hypothetical pore space lined with a layer of chemically bound oriented wax molecules. Index ellipses of the residual double refraction caused by these molecules, are indicated.

the three layers visible in sections (fig. 7c), but the residual double refraction differs in character. The positive residual birefringence of the inner layer might be due to cellulose-fibrils, but regarding the outer layer we have no explanation.

Using electron diffraction methods, HURST (1950) demonstrated the presence of non-extractable, heat-stabile oriented lipids in insect cuticles. This tallies with our postulation concerning plant cuticles.

§ 4. RESIDUAL INTRINSIC DOUBLE REFRACTION IN CUTICULAR LAYERS OF OTHER PLANTS

As discussed in section 2c, MEYERS' sections of *Clivia nobilis* were isotropic after removal or destruction of the waxes, whereas ours were not. It was of some interest to find out whether the same divergence of results could be found in the other objects studied by her.

Axial and transverse sections of 20 μ thickness were therefore cut from the leaves of *Gasteria trigona*, *Dasylirion serratifolium*, *Yucca aloifolia* and *Aloe glauca*. After dehydrating with abs. alcohol and mounting in benzene the optical properties were studied. They were then extracted with boiling pyridine for 5 days, bleached with hypochlorite, dehydrated, mounted in benzene and examined again.

The cuticular membranes showed two distinctly different double refractive layers. In *Gasteria* the outer one is reminiscent of the outermost thin layer in *Clivia*, which we called cuticle. In *Dasylirion* and *Aloe* in addition an isotropic cuticle seems present. We will however, leave aside these questions and distinguish an outer and inner cuticular membrane. Their optical properties before and after extraction are given in table 2.

TABLE 2

Character (with resp. to leaf surface) of double refraction of different cuticular layers in sections before and after extraction of waxes. Between brackets: results of MEYER (*l.c.*)

Object	Cuticular membranes				Ridge between cells	
	before extraction		after extraction		before extr.	after extr.
	inner	outer	inner	outer		
Gasteria	— (—)	— (—)	+ (+)	— (0)	+	—
Dasylirion	+,0 (+)	— (—)	+ (+)	— (0)	+	—
Yucca	+ (0)	— (—)	+ (+)	— (0)	+	+
Aloe	+	—	+	—	+	0

The small differences between MEYERS' and our results in the first column may be due to the use of different plants, containing different wax or cellulose quantities in their cuticular membranes. The fourth column, however, shows that in all these plants, as also in *Clivia*, a residual intrinsic double refraction was visible after extraction of waxes. It was by no means a faint double refraction as will become apparent on examination of the figs. 12a, b, and 13a, b, each of which shows a photomicrograph between crossed nicols and a photomicrograph of the same spot after compensating the double refraction in the outer layer with the elliptic compensator. In every case the double refraction of the inner layer is increased when the outer layer is compensated, which proves that their doubly refractive character is opposite. A similar explanation as given for *Clivia nobilis*, must be accepted here.

SUMMARY

By dissolving the cutin in hot alcoholic alkali, the cellulose "skeleton" from the cuticular layer of *Clivia nobilis* leaves has been isolated (fig. 2) and the fibril orientation therein has been determined (fig. 3).

The form double refraction of wax-free cuticular membranes of *Clivia nobilis* indicates the presence of emptied oblong flat pores, tangentially oriented and with their major axis transversal (fig. 9). The wax platelets are mainly tangentially oriented too, but these probably have a preference for slight transverse inclinations (fig. 10). thus producing a corresponding double refraction in surface view. The cuticle *sensu stricto*, up till now considered isotropic, is birefringent too (fig. 6).

After extraction or heat-destruction of true waxes the major part of the cuticular membrane still shows a faint double refraction with a radially oriented major refractive index (fig. 7). This is tentatively ascribed to chemically bound oriented wax molecules, lining the pore space (fig. 11). A similar state of affairs occurs in the cuticular membranes of *Gasteria*, *Yucca*, *Dasylirion* and *Aloe*.

ACKNOWLEDGEMENT

We are greatly indebted to Prof. L. J. Audus for correction of the English text.

REFERENCES

ANDERSON, D. B. Struktur und Chemismus der Epidermisauszenwände von *Clivia nobilis*, Jahrb. f. Wiss. Bot. *69*, 501, (1928).

FREY, A. Die submikroskopische Struktur der Zellmembran. Jahrb. f. Wiss. Bot. *65*, 195, (1926).

HURST, H. An electron diffraction study of the crystalline structure of the lipids in the pupal exuviae of *Calliphora erythrocephala*, J. Exp. Biol. *27*, 238. (1950.)

KREGER, D. An X-ray study of waxy coatings from plants. Rec. tr. botan. néerl. *41*, 603, (1948).

LAVES, F., TH. ERNST. Die Sichtbarmachung des Charakters (+ bzw —) äuszert schwacher Doppelbrechungseffekte. Naturwissenschaften *31*, 68, (1943).

MEYER, M. Die submikroskopische Struktur der kutinizierten Zellmembranen. Protoplasma *29*, 552, (1938).

ROELOFSEN, P. A., A. L. HOUWINK Cell wall structure of staminal hairs of *Tradescantia virginica* and its relation with growth. Protoplasma *40*, 1, (1951).

WEBER, E. über die Optik und die Struktur der Pflanzenwachse. Ber. Schweiz Bot. Ges. *52*, 112, (1942).

WISSELINGH, C. VAN. Mikrochemische Untersuchungen über die Zellwände der Fungi. Jahrb. f. wiss. Botan. *31*, 619, (1898).

APHANES MICROCARPA IN THE NETHERLANDS

BY

TH. REICHGELT

Received October 3, 1951

A few years ago I was struck by the mention in RAUNKIAER's Dansk Ekskursionsflora (1942), of *Aphanes microcarpa* (Boiss. et Reut.) Rothm. (= *Alchemilla microcarpa* Boiss. et Reut.) as occurring in Denmark, whilst in ASCHERSON and GRAEBNER, Synopsis VI (1900—1905) only Spain is mentioned. RAUNKIAER's publication led me to think of the possibility of the occurrence of this species, which strongly resembles *Aphanes arvensis* L, in the Netherlands too. It was not until early in 1950, when I came across the statement in S. M. WALTERS' article on the occurrence of *A. microcarpa* in Britain, in Watsonia (Vol.I., Part III, 1949), that this species shows a preference for acid soils, that I was induced to go further into the matter. The first corn-fields I investigated, situated on the edge of the Wychen fen, yielded it, and in the next few weeks it was copiously collected in several localities in the vicinity of Nimeguen, so that it did not seem unjustified to presume that it would occur rather frequently in the Netherlands.

A short summary of the history of the species may be inserted here. It was first distinguished by BOISSIER and REUTER (in Diagn. pl. nov. hisp.) in 1842, and described from Spanish specimens. In 1935 ROTHMALER (lit. 1) mentions it from Italy, Algeria, Morocco, Southern France, Spain, Portugal, Madeira, the Canaries, and the Azores, and from a separate area around Constantinople. In addition it is stated to occur in the Eastern United States.

In 1937 WALO KOCH (lit. 2) states the species to occur in a few places in Switzerland.

In the same year a paper was published by NYLANDER and ROTHMALER (lit. 3) from which we learn that *Aphanes microcarpa* is of very frequent occurrence in the Southern part of Sweden; it is further mentioned from Bulgaria, Czechoslovakia, Germany and Denmark (in the latter country 2 stations are known).

In 1941 GUDJONSSON publishes a paper (lit. 4) in which it is shown that in Denmark the species is as common as *A. arvensis.*

The year 1949 sees the publication of WALTERS' article, mentioned already (lit. 5), from which it is clear that in England too *A. microcarpa* is frequent.

Lastly, in 1950, A. LAWALRÉE (lit. 6) ascertains the occurrence of the species in Belgium, so far only in one locality, situated in the Campine. In all non-mediterranean countries enumerated, including ours, it had simply been taken for granted that *A. arvensis* only would be present. As a matter of fact, the differences between the two species are not great and the small size and inconspicuousness of the plants may have played a part as well.

The main differences between the species are best seen in fruiting plants. The fruits * of *A. arvensis* are almost twice as long as those of *A. microcarpa*; WALTERS indicates for *A. microcarpa* 1.4—1.8 mm, for *A. arvensis* 2.2—2.6 mm. The calyx-teeth likewise are much longer in *A. arvensis* than in *A. microcarpa*, and as a rule distinctly spreading, the calyx is somewhat constricted beneath the teeth, so that the whole is slightly bottle-shaped, whereas the calyx-teeth in *A. microcarpa* usually converge so that the fruit shows an oval outline.

The achene too is smaller in *microcarpa* than in *arvensis*, and in addition I noticed a difference which I have not found mentioned in any of the publications consulted: the colour of the ripe achene is light, dirty yellow in *microcarpa*, but darker, brown, in *arvensis*. In the Dutch specimens examined I have not found any exception to this rule. It remains to be seen, of course, if this character will prove universally distinctive, but it seems probable to me.

Another important character may be found in the shape of the stipules enwrapping the inflorescence. As a rule these are in *A. arvensis* by no means as deeply dissected as in *A. microcarpa*; their segments are long and narrow in *microcarpa*, shorter and wider, rather triangular, in typical *arvensis* (cf. fig.). But it cannot be denied that especially *arvensis* is rather variable with regard to this character — as has been observed by GUDJONSSON too — and sometimes it closely approaches *microcarpa*. Yet the character is in most cases quite serviceable. In herbarium specimens, which, fortunately, are almost invariably collected in the fruiting stage, both species are often recognizable at a glance because of the large fruits of *arvensis* distinctly overtopping the teeth of the stipules. In *microcarpa* this is very rarely seen; in the large majority of cases the achenes are hidden between the stipules and only here and there the top of the calyx is seen protruding from amongst the segments of the stipules.

The following differential characters are less obvious.

According to NYLANDER and ROTHMALER the colour of the whole plant is greyish-green in *arvensis*, but yellowish-green in *microcarpa*. GUDJONSSON, although he has often found both species growing side by side, has failed to ascertain any conspicuous difference in colour.

WALTERS, on the contrary, asserts that there is a slight difference in colour. As to my own experience, I can say that as a rule *microcarpa* is pure green, and *arvensis* often greyish green, but frequently it is almost impossible to ascertain any difference in colour.

If well developed plants of both species are compared side by side, it can be seen also that *A. microcarpa* is more slender than *A. arvensis*, a character which in most cases enabled me, when perusing herbarium specimens, to make at a glance a provisional separation between both species, which often had been mounted together on one sheet.

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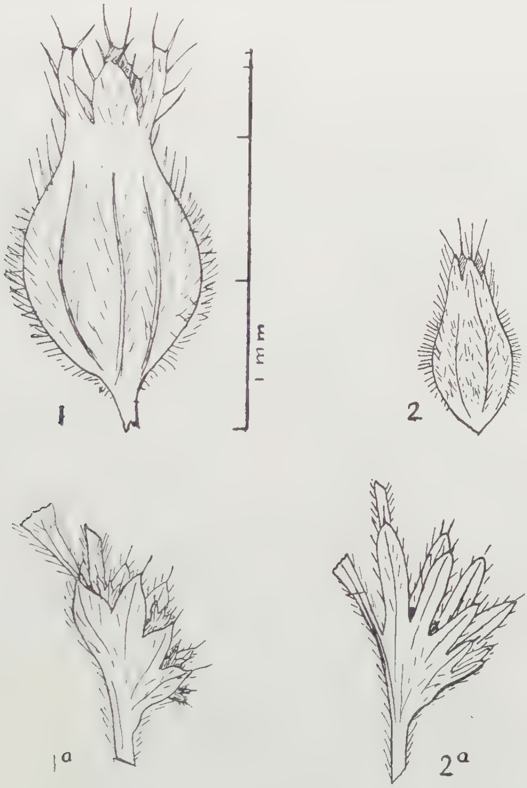
* For convenience of expression the term "fruit" is used throughout the paper as denoting the body formed by the urceole, the achene and the persisting calyx.

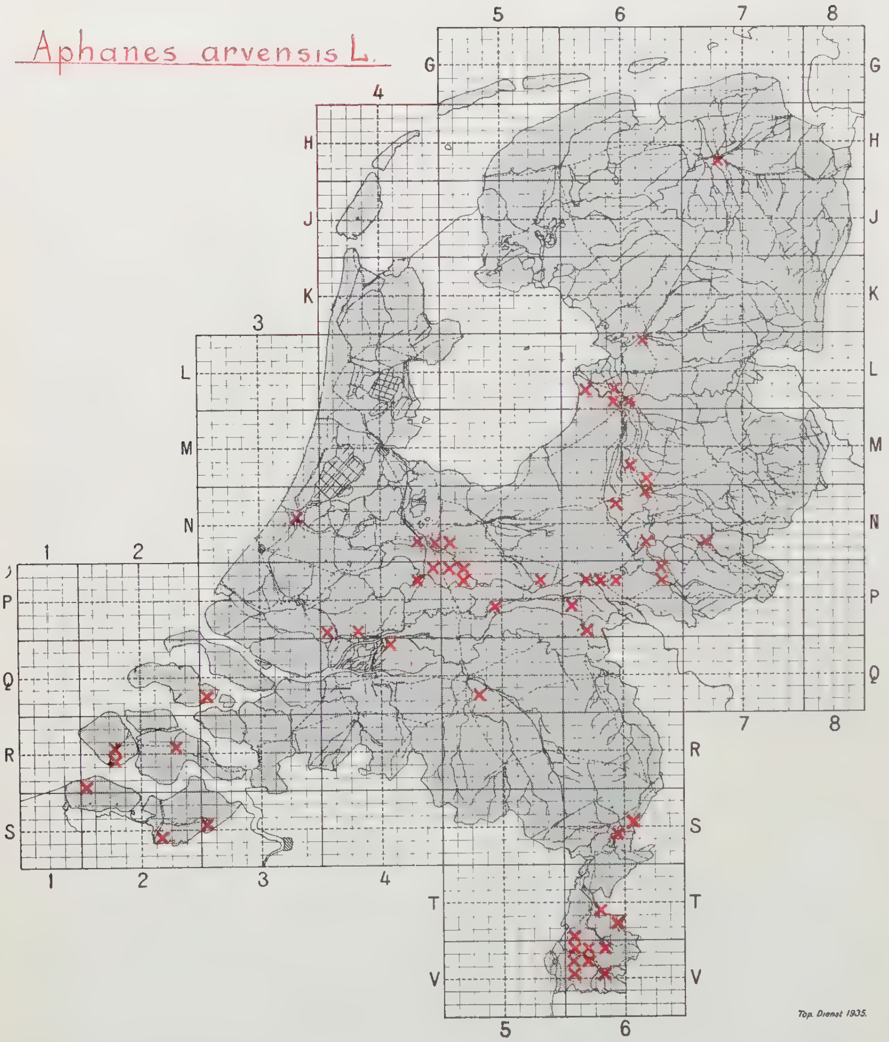
Gudjonsson records a difference in flowering time; *A. microcarpa* flowers later than *A. arvensis*. This is in accordance with my experience; the first plants of *microcarpa* which I collected in 1950 were just beginning to develop their fruits, whereas specimens of *A. arvensis*, which I collected the same day for the purpose of comparison, showed an abundance of developed fruits and later in the year, at a time when *A. arvensis* had almost completely died down, I still found specimens of *A. microcarpa* in full flower.

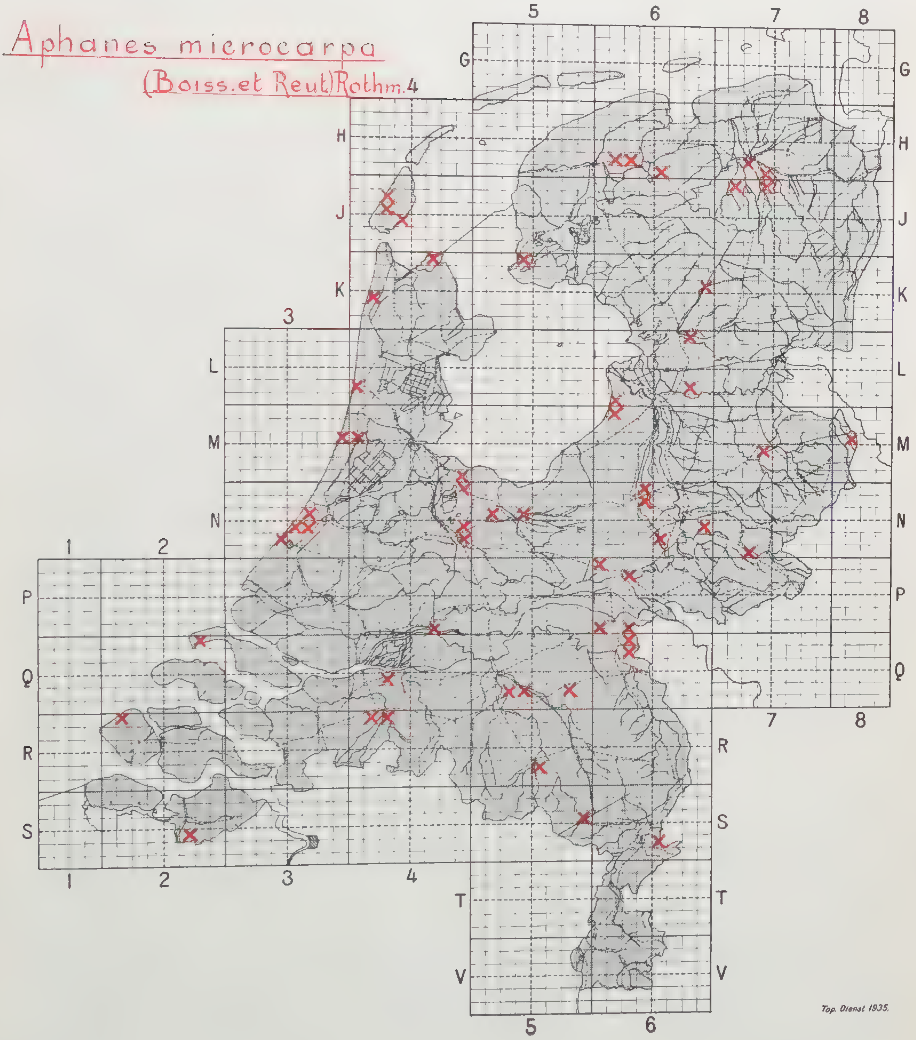


Fruit and fruiting inflorescence of *Aphanes arvensis* (1, 1a), as compared with those of *A. microcarpa* (2, 2a)

The conclusions which can be drawn from the herbarium specimens seen by me, relating to the distribution of both species in our country must bear a provisional character on account of the limited material available. The total number of sheets examined is 193, taken from the collections of the "Koninklijke Nederlandsche Botanische Vereeniging", the State Herbarium at Leyden, and the Universities of Amsterdam, Utrecht and Groningen, and from the private herbariums of van Soest, Kloos and Kern and Reichgelt. It appears that *A.*

Aphanes arvensis L.




Aphanes microcarpa
(Boiss.et Reut.)Rothm.
1
2
3
4
5
6
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L
M
N
P
Q
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V
Top. Dienst 1935.

arvensis has been collected 96 times, as against *microcarpa* 84 times, so that the former can scarcely be called a more common plant than the latter. If the number of stations is considered even the reverse seems true, viz. 52 of *arvensis* against 57 of *microcarpa*. If the stations (cf. the maps) are arranged according to the provinces it turns out that in Friesland, Drente and North-Holland *microcarpa* only has been found, whilst in the remaining 8 provinces both species occur. If arranged according to the phytogeographical districts of VAN SOEST (lit. 7) the picture becomes somewhat more distinct: in the Chalk and Loess districts only *A. arvensis* has been found; in the River and "Haff" districts this species is predominating, but in the Dune and "Wadden" districts it is probably absent.

A. microcarpa, on the contrary, is probably the only species occurring in the Dune and "Wadden" districts; it predominates in the Drente and Campine districts, and is wanting in the Chalk and Loess districts. In the Guelder and Subcentreurope districts both species occur in an equal number of stations. Although this result must be prudently handled, for the data available from certain districts are very few, it justifies nevertheless a provisional conclusion which corroborates the experiences of GUDJONSSON in Denmark and WALTERS in Britain.

Both species, which are found in the mediterranean region in heaths and steppes, do not occur here nor elsewhere in M. an N. Europe in natural vegetations; they grow in cultivated fields only.

NYLANDER and ROTHMALER were unable to ascertain a distinct difference in the Swedish habitats of both species, but GUDJONSSON did so for Denmark and concluded that *A. microcarpa* clearly dominates in the oligotrophous parts of the country, whereas *A. arvensis* is the more frequent species in the eutrophous, calcareous regions. In the transitional zones they may both occur in the same field, or be found alternatingly in different stations according to the character of the soil. GUDJONSSON relates indeed that he could predict, with very few failures, which of both species would be found in any field he happened to pass by.

WALTERS likewise concludes for Britain that his data strongly point to the probability that "*A. microcarpa* is more or less restricted to acid soils ,whilst *A. arvensis* appears to be indifferent to soil acidity". From the picture of the distribution of both species, as outlined above according to the districts of VAN SOEST, it can be said that in the Netherlands likewise *A. arvensis* predominates in the rich and often calcareous fields of the Loess, Chalk and River districts, whereas *A. microcarpa* is found mainly in the poor, often acid fields of the Drente, Campine, Dune and "Wadden" districts. Also my personal experience in the Nimeguen region agrees in the main with what has been found by GUDJONSSON.

The specimens which, according to the labels, had doubtless been collected in the Dunes, belong all to *A. microcarpa*, but all of them are of a type which slightly differs from *A. microcarpa* as found elsewhere in the Netherlands. The plants are small-leaved, and their stipules are very short so that, in contradistinction to the plants hailing from other parts of the country, the achenes often protrude from the stipules. It seems quite possible to me that these plants from the dunes are to be considered as belonging to a separate variety, but this remains to be established until cultural experiments have taught us something on the constancy of these characters under varying conditions. In the literature accessible to me I did not find anything worth mentioning about varieties of *A. microcarpa.*

Gudjonsson has also investigated the cytology of both species, and found for *A. microcarpa* 2n = 16, for *A. arvensis* 2n = 48, and Walters mentions, as the result of an examination by Gustafsson in 1948, that "*A. microcarpa* is sexual and diploid with 2n = c.16, whilst *A. arvensis* is polyploid with 2n = c.48, but reproduces agamospermously".

In conclusion I may be allowed to explain why I deviate from the nomenclature so far usual in our country.

Rothmaler, in 1935, still considers *Aphanes* a subgenus of *Alchemilla*, besides *Eualchemilla* (Focke) Buser and *Lachemilla* (Focke) Lagerh. In 1937, however, he treats these subgenera as genera, and, as a matter of fact, there are very considerable differences between *Alchemilla* and *Aphanes*. *Aphanes* has only one stamen, inserted, opposite a sepal, on the inner margin of the disk, and carrying an extrorse anther, whereas *Alchemilla* shows four stamens, alternating with the sepals, inserted on the outer margin of the disk and having introrse anthers. In addition there is a considerable difference in habit: all *Alchemilla* species are perennial and rhizomatous, all *Aphanes* species are annuals with fibrous roots only. The build of the inflorescence too is widely different. In the Scandinavian floras *Aphanes* is treated as a separate genus, and also Walters in Britain and Lawalrée in Belgium follow Rothmaler in this respect. There seems every reason for us to conform to this practice and to reinstate *Aphanes* in its original rank.

REFERENCES

1. Rothmaler, Werner., Systematische Vorarbeiten zu einer Monographie der Gattung *Alchemilla* (L) Scop. emend. Fedde Repertorium, Band XXXVIII p. 33—43, (1935).
2. Koch, Walo., *Alchemilla microcarpa* Boissier et Reuter als neue Schweizerpflanze. Berichte der Schweizerischen Botanischen Gesellschaft, Band 47, p. 443—445, (1937).
3. Nylander, Nils och Rothmaler, Werner., Om *Aphanes microcarpa* (Boiss. et Reut.) Roth., en hittils förbisedd svensk växt, och dess förhällande till *A. arvensis* L. Svensk Botanisk Tidskrift. Bd. 31 p. 411—424. (1937).
4. Gudjonsson, Gudni., Om *Aphanes arvensis* L. og *A. microcarpa* (Boiss. et Reut.) Rothm. og deres Udbredelse i Danmark. Botanisk Tidskrift Bd. 45, p. 352—370 (1941).
5. Walters, S. M., *Aphanes microcarpa* (Boiss. et Reut.) Rothm. in Britain. Watsonia Vol. I Part III, p. 163—168, (1949).
6. Lawalrée, André., Les *Aphanes* de la flore belge. Bull. de la Soc. Royale de Botanique de Belgique. T. 83, p. 129—132, (1950).
7. Soest, J. L. van., Plantengeografische districten van Nederland, in Heukels, Geïllustreerde Schoolflora voor Nederland. 13. ed. p. 7—8, (1949).

AANWINSTEN VAN DE NEDERLANDSE FLORA IN 1950

(ACQUISITIONS TO THE FLORA OF THE NETHERLANDS IN 1950)

DOOR

A. W. KLOOS Jr.

Een deel van de hier volgende nummers is van de hand van
Dr S. J. van Ooststroom *te Leiden*

Received October 3, 1951

1. **Brachiaria eruciformis** (J. E. Sm.) Griseb. in Ledeb. Fl. Ross. 4 (1853) p. 469.

Het voor ons land nieuwe geslacht *Brachiaria* behoort tot de Gramineeën-Tribus *Paniceae* en werd vroeger als een afdeling van het geslacht *Panicum* beschouwd. In The Grasses of Mauritius and Rodriguez by C. E. Hubbard and R. E. Vaughan (1940) p. 24 voeren de volgende eigenschappen tot het geslacht:

"Spikelets not subtended by bristles.
  Upper glume and lower lemma usually entire at their tips.
    Lower glume awnless, spikelets circular in transverse section or often dorsally compressed.
      Upper floret alone fertile, the lower male or barren, its lemma resembling the upper glume and usually not hardened.
        Spikelets arranged in one-sided spikes or spike-like racemes, not subtended by bristles.
          Lemma of the upper floret more or less coriaceous with narrow inrolled margins, exposing much of the palea.
            Lower glume usually well developed; lower floret ♂ or barren.
              Upper glume acute or obtuse, smooth or hairy.
                Axes of racemes terminating in a spikelet.
                  Lower glume adjacent to the axis on which the spikelet is borne; upper lemma often obtuse and rarely mucronate . . . . *Brachiaria.*"

De beschrijving van het geslacht luidt dan l.c. p. 75:

"Spikelets oblong to lanceolate, ovate or elliptic, awnless, terete or more or less dorsally compressed and then flattened in front, solitary, paired or clustered, falling entire at maturity, short-pedicelled or almost sessile along one side of the 3-angled or flattened axes of spike-like racemes; florets 2, dissimilar, the lower ♂ or barren and with a palea, the upper ⚥; glumes membranous, equal or more often unequal, the lower smaller and adjacent to the axis on which the spikelet is borne; the upper as long as the spikelet and similar to the lower lemma; upper lemma obtuse, apiculate or mucronate, crustaceous or coriaceous, with narrowly involute margins embracing the indurated palea. Perennials or annuals, with loosely to densely spiculate racemes."

Tot de soort komt men dan door:

"Lower glume $^1/_6$—$^1/_2$ the length of the spikelet; spikelets elliptic to elliptic-oblong or ovate-elliptic or obovate, 1,5—3,5 mm long.
  Inflorescence 2—20 cm long, composed of few to many racemes, bearing numerous spikelets; leaf-blades 1—30 cm or more long.
    Spikelets solitary.
      Spikelets 2—2,5 mm long, elliptic-oblong, hairy; inflorescence with 5—12 racemes; tufted annual . . . . *B. eruciformis*."

die dan l.c. p. 79 beschreven wordt:

"**B. eruciformis** (J. E. Sm.) Griseb. in Ledeb. Fl. Ross. **4**, 469 (1853). *Panicum eruciforme* J. E. Sm. in Sibth. & J. E. Sm. Fl. Graeca, **1**, 44, t. 59 (1806); Fl. M. & S. 434. *Panicum Isachne* Roth ex Roem. & Schult. Syst. Veg. **2**, 458 (1817). *P. anisostachium* Bojer, Hort. Maurit. 364 (1837), name only. *Brachiaria Isachne* (Roth) Stapf in Prain, Fl. Trop. Afr. **9**, 552 (1919).

A loosely tufted annual, 15—60 cm high; culms geniculately ascending, often from a decumbent base and rooting at the nodes, very slender, branched, glabrous; leaf-sheaths softly hairy, or glabrous except for the densely hairy nodes; ligule a densely hairy rim; blades narrowly lanceolate or linear-lanceolate, acute, 1,5—10 cm long, 2—6 mm wide, flat, hairy or glabrous; inflorescence narrow, contracted, 2—10 cm long; racemes 5—12, erect and appressed to the main axis, or slightly curved, dense, 1—2,5 cm long, their axes about 0,3 mm wide; pedicels very short; spikelets solitary, elliptic-oblong, obtuse, 2—2,5 mm long, softly hairy; lower glume minute and nerveless; upper glume 5-nerved; upper lemma obtuse, smooth and shining. Chromosome no. $2n = 18$.

Cane-fields and waste places, in districts with medium rainfall.

Exsicc. — *Bojer. Bouton* G. 56. *Du Petit-Thouars. Herb. Maurit.* A. 127. *Vaughan* A. 24, A. 75, A. 76.

Rodriguez, Réunion; native in Spain eastwards to India, north-east tropical Africa and South Africa; introduced elsewhere."

Op 11 Aug. 1950 verzamelde ik de soort te Tilburg bij een wol- en huidenfabriek, tussen een dichte menigte hoogopgeschoten andere woladventieven.

PROBST geeft in Wolladventivflora Mitteleuropa's (1949) p. 6 de vindplaatsen: Osnabrück, Kettwig en Leipzig aan.

ASCHERSON & GRAEBNER geven in Syn. II. 1 (1902) p. 68 de vindplaats Berlin.

Dr P. JANSEN, die bij mijn plant de notitie voegde "Een schaduw-vorm van een jonge plant, die nog het meeste heeft van *Brachiaria eruciformis* (J. E. Sm.) Griseb. ongevleugelde spil, 1e kelkkafje zeer klein tot ontbrekend, rechtop staande zijaren en zacht behaarde aartjes" meldt mij verder, dat hij de soort al eens eer te Amsterdam gevonden heeft, maar door omstandigheden nog niet opgegeven.

2. **Psilurus aristatus** (L.) Duv.-Jouve, Bull. S. B. Fr. XIII (1866) p. 132. Het geslacht *Psilurus* behoort met *Lepturus*, *Parapholis* en *Pholiurus* tot de Tribus *Monermeae*. Het komt met *Lepturus* daarin overeen, dat elk zijdelings aartje slechts één kelkkafje heeft. Terwijl dit kelkkafje bij *Lepturus* echter het gehele aartje bedekt, is het bij *Psilurus* veel korter dan het kroonkafje van de onderste bloem. De beschrijving van het geslacht bij Rouy Fl. de Fr. XIV (1913) p. 341 luidt: "Epillets un peu écartés du rachis scabre pendant l'anthèse puis strictement cachés dans ses excavations, lancéolés-subulés, 1—3-flores, espacés, formant un épi dressé, arqué ou flexueux, très long et filiforme, fragile; fleur inf. sessile, hermaphrodite, la 2me et la 3me ordt. stériles ou rudimentaires. Glume unique sur les épillets latéraux, très petite (5—6 fois plus courte que la fleur inf.), ovale, aigue, glabre ou brièvt-ciliée; épillet terminal à 2 glumes inégales, courtes. Glumelle inf. coriace, souvent violacée, acuminée, uninervée, très rude, aristée; la sup. bicarénée, bidentée, rude sur les carènes, égalant à peu près l'inf. (moins l'arête). Glumellules 2, ovales-lancéolées, glabres. Etamine unique. Caryopse linéaire-cylindracé, canaliculé sur la face interne." Ascherson und Graebner geven in Syn. Mitt. Eur. Fl. II. 1 (1902) p. 766 de beschrijving: "Der vorigen Gattung (*Pholiurus*) ziemlich ähnliches einjähriges Gras mit sehr dünner, fast einer Blattspreite gleichender schlanker und zarter Aehre. Aehrchen einblüthig oder an der Verlängerung der Aehrchenachse noch eine zweite Blüthe tragend, der Achse stark angedrückt, nicht eingesenkt. Hüllspelze sehr kurz, Deckspelzen aus der Spitze fein begrannt. Jede Blüthe mit nur einem Staubblatt".

De soort beschrijft Rouy l.c.: "**P. nardoides** Trin.; *P. aristatus* Duval-J.; *Nardus aristata* L.; *Festuca filiformis* Pourr.; *Rottboellia monandra* Cav.; *Asprella nardiformis* Host; *Monerma monandra* P. B.–Tiges de 1—3 déc., genouillées-redressées ou dressées, très grêles ou subfiliformes, fasciculées. Feuilles courtes, fines, enroulées-subulées, glabres, lisses à l'ext., rudes à l'int., gaine sup. entourant la partie inf. de l'épi; ligule très courte, tronquée. Glume parfois nulle dans les épillets lat. Glumelle inf. dépassant de beaucoup la glume. ⊙ Mai-juin.

Hab.–Coteaux arides, lieux incultes et sablonneux du midi. Rég. méditerr., Cévennes; sud-est; Rhône: Oullins, Montchat, Empuis; Corse. Aire géogr. Europa mérid.; Asie austro-occid.; Afrique septentrionale." en A. & G. l.c.: "**P. aristatus** ⊙ Pflanze am Grunde büschelig verzweigt, meist zahlreiche aufrechte oder aufsteigende sehr dünne, selten bis über 3 dm lange Stengel treibend. Blätter mit glatter Scheide und sehr feiner borstlicher Spreite. Blatthäutchen kurz, eiförmig, kaum 1 mm lang. Aehre bis fast 2 dm lang, sehr dünn, kaum

1 mm dick, mit meist einmal bis mehrmals gebogener und meist, wenigstens zuletzt, deutlich gedrehter, halbstielrunder, kahler oder fein rauher Achse. Aehrchen schmal linealisch-lanzettlich, kahl oder fein rauh, ohne die Granne etwa 5 mm lang. Deckspelze ganz schmal, mit etwa 3—6 mm langer, sehr dünner Granne, rauh. Hüllspelze nur 1 mm oder wenig länger.

An trockenen, unfruchtbaren Orten im Mittelmeergebiete: Riviera; Provence, Dauphiné, im Rhônethal bis Lyon. Venetien in den Provinzen Verona, Vicenza, Treviso, Udine. Oesterr. Küstenland, Istrien, nebst den Inseln, Kroatien, Dalmatien. Unt. Donauthal. Im übrigen Gebiete sehr selten eingeschleppt; Hamburg: Wollkämmerei an Reiherstieg 1895."

Op 8 Juni 1950 vond ik bij de Tilburgse Wolwasserij een graspol, die mij vreemd voorkwam en die ik meenam om in mijn tuin, zo mogelijk, in bloei te krijgen. Toen ik thuis echter de plant beter bekeek, bleek zij in volle bloei te zijn en bracht determinatie mij tot *Psilurus aristatus*. PROBST noemt het geslacht in zijn Wolladventivflora Mitteleuropas niet.

3. **Chenopodium carinatum** R. Br. var. **holopterum** (Thell.) Aellen. det. PAUL AELLEN. Toen ik in "Aanwinsten 1940" in Ned. Kruidk. Arch. 51 (1941) p. 103 de vondst van *Chenopodium pumilio* R. Br. vermeldde, gaf ik daarbij ook de beschrijving van *Ch. carinatum* R. Br. en ter onderscheiding van de beide soorten het extract uit de determinatietabel in BENTHAM and MUELLER: Fl. Austr. V (1870) p. 158:

> "Perianth-segments broad, concave with a thickened keel . . . . *C. carinatum.*
> Perianth-segments narrow, nearly erect with a thickened keel, minute filiform plant . . . . *C. pumilio.*"

Op 12 Juli 1950 vond ik bij de Tilburgse Wolwasserij een nog niet bloeiende *Chenopodium*, die ik naar Dordrecht overbracht en waarvan ik in September volledig materiaal verzamelde. Een tak daarvan zond ik aan AELLEN, die haar determineerde als *C. carinatum* var. *holopterum* (Thell.) Aellen. Deze var. werd door THELLUNG gepubliceerd in zijn artikel: Beiträge zur Adventivflora der Schweiz III in Viertel ahrss, Natforsch. Ges. in Zürich LXIV (1919) p. 724 onder *Ch. cristatum* F. v. Muell.:

"var. (?) *holopterum* Thell. f. nov. (ala tepalorum subintegerrima, a latere visa triangulari, appendicibus fimbriiformibus dorsalibus et processu aristiformi terminali plane destituta. An species propria? an proles hybrida: *Ch. carinatum* × *cristatum*? Differt a *Ch. carinato* carina tepalorum in alam longitudinalem tenuem triangularem producta nec obtuse naviculari). Flügel der Perianthblätter (von der Seite gesehen) dreieckig, fast ganzrandig, gleichsam auf den Grundkörper reduziert, ohne dorsale fransenförmige Anhangsgebilde und ohne grannenartige Endspitze. Mit dem Typus der Art und mit *Ch. carinatum*, in wenigen Exemplaren, 1917. PROBST! Bei der Spärlichkeit des

Materials lässt sich ein endgültiges Urteil über den Wert dieser auffallenden Sippe noch nicht abgeben. Sofern man nicht eine besondere Art anzunehmen geneigt ist, liegt der Gedanke an einen Bastard (*C. carinatum* × *cristatum*) oder noch mehr an eine Abart von *Ch. cristatum* nahe, bei welcher Spezies möglicherweise die der zoochoren Verbreitung dienenden Anhangsgebilde der Perianthblätter, ähnlich den Früchten vieler *Medicago*-Arten, starke Schwankungen in der Ausbildung aufweisen und unter Umständen gänzlich verkümmert sein können."

In zijn artikel Die wolladventiven Chenopodien Europas, Verh. Naturf. Ges. Basel XLI (1930) noemt Aellen p. 99: *Ch. holopterum* (Thell.) Thellung et Aellen als afzonderlijke soort naast *Ch. carinatum* R. Br. en *Ch. cristatum* F. v. M. om ten slotte in: Die Arten der Sect. *Orthosporum* R. Br. der Gattung *Chenopodium* L. in Verh. Naturf. Ges. Basel XLIV, 1 (1933) p. 312 tot de combinatie *Ch. carinatum* R. Br. var. *holopterum* (Thell.) Aellen te komen. Volgens Probst Wolladventivflora Mitteleuropas (1949) p. 62 is deze vorm als woladventief bekend uit Zwitserland, Elzas, Schotland, Zweden en Duitsland.

4. **Amaranthus angustifolius** Lam. var. **polygonoides** (Roxb.) Thell. f. **latifolius** Thell. in Asch. et Gr. Syn. V (1914) p. 309. Van de soort *A. angustifolius* waren tot nog toe in ons land alleen waargenomen de var. *silvester* (Desf.) Thell. (vrij algemeen) en var. *graecizans* (L.) Thell. (zeer zeldzaam). De var. *polygonoides* (Roxb.) Thell. onderscheidt zich van de beide vorige volgens Thellung l.c. p. 308 door: "Weibliche Perigonblätter lanzettlich-pfriemlich, lang zugespitzt, mit deutlich hervortretender, etwa (1/4) 1/3—3/4 mm langer Stachelspitze; Vorblätter von ähnlicher Gestalt, meist noch länger grannenspitzig, mit der Spitze meist so lang oder selbst etwas länger als das Perigon.

In der Tracht der Rasse *graecizans* ähnlich. Durch die langen Grannenspitzen der Perigonblätter, die zuweilen die Spitze der Frucht erreichen oder selbst etwas überragen, erinnert die Rasse einigermaassen an *A. Dinteri*, von dem sie sich jedoch durch die abweichenden Behaarungsverhältnisse und die auffallend schmalen, im oberen Theil fast völlig auf den schmalen Mittelnerv reducirten weiblichen Perigonblätter leicht unterscheidet.

Heimisch im tropischen Africa und Asien; bei uns sehr selten eingeschleppt.

Eine einigermaassen kritische Pflanze, die man als Unterrasse an *graecizans* anzugliedern versucht sein könnte, wenn nicht die Abart *latifolius* in der Blattform (wenigstens in der Breite) der Rasse *silvester* näher stünde. Der Bearbeiter hatte die letztere Abart ursprünglich in seinen Bestimmungen (Herb. Höppner) als *A. silvester aristatus* bezeichnet; doch gehören die 3 im Folgenden genannten Abarten, wie auch ihr gemeinsames Vorkommen an der Adventivfundstelle Neuss bekräftigt, sicherlich phylogenetisch nahe zusammen, so dass es angezeigt erscheint, sie zusammengefasst als besondere Rasse den beiden vorhergehenden gegenüberzustellen.

Aendert nach der Blattform:
I. *latifolius* (Thellung in A. u. G. Syn. V [1914]. — *A. silvester* var. *aristatus* Thellung in Herb. Höppner). Laubblätter elliptisch oder verkehrt-eiförmig, etwa 2 mal zo lang als breit."
Prachtig materiaal groeide in 1950 te Tilburg op het terrein van de Tilburgse Wolwasserij, waarvan ik verzamelde op 11 Augustus. Ook in Engeland is de var. *polygonoides* adventief waargenomen. BARRY leg. DRUCE in Herb. Oxford.

5. **Papaver rhoeas** L. var. **pryorii** Druce (door S. J. VAN OOSTSTROOM).
Exemplaren van deze variëteit, die gekenmerkt is door de opvallend rode, afstaande beharing, vooral op de bloemstelen, werden aangetroffen tussen talloze normale planten en exemplaren van de var. *strigosum* Boenningh. te Lent, langs de autoweg naar Arnhem door Dr B. K. BOOM op 26 Mei 1950 (H.L.B. 950. 325—179).

6. **Monsonia brevirostrata** R. Kunth in Engler's Bot. Jahrb. XL (1907) p. 67. Op 18 Juli 1928 vonden PATER LUDOVICUS en KLOOS bij de wol- en huidenfabriek der firma PESSERS–VERBUNT te Tilburg een plant, die wij voorlopig als *Erodium malacoides* determineerden en waarvan onder die naam een foto is gereproduceerd in de Levende Natuur 43 (1939) p. 277. Dergelijke planten werden op hetzelfde terrein of op het aangrenzende van de firma BERN. PESSERS gevonden in 1941, 1947, 1948 en 1950, maar de determinatie bevredigde mij hoe langer hoe minder. Naar aanleiding van deze laatste vondst hebben VAN OOSTSTROOM en ik in het Rijksherbarium te Leiden nog eens een grondig onderzoek ingesteld. In de eerste plaats hebben wij al het aanwezige materiaal van *Erodium malacoides* nog eens doorgenomen, waarbij bleek, dat er geen enkel exemplaar aanwezig was, dat met de Tilburgse planten overeenkomt. Ook waren er geen verwante *Erodium*-soorten, die in aanmerking konden komen. Met behulp van de monographie der *Geraniaceae* van R. KUNTH in ENGLERS Pflanzenreich IV. 129 (1912) bleken de Tilburgse planten te behoren tot het geslacht *Monsonia* L., dat van *Erodium* verschilt, doordat de bloem 15 meeldraden heeft, die in 5 groepen van 3 geplaatst zijn, elk drietal aan de voet met elkaar verbonden. De beschrijving van het geslacht luidt bij KUNTH l.c. (1912) p. 290:
"*Monsonia* L. (Nomen a L. generi datum in honorem virginis ANNA MONSON amicae cl. autoris) Flores regulares. Sepala 5, imbricata. Petala 5, hypogyna, imbricata. Glandulae 5, petalis alternae. Stamina 15, omnia antherifera, brevissime in annulum connata; trina inter sese altius coniuncta et sepalis opposita. Ovarium 5-lobum, 5-loculare, rostratum, apice ramis introrsum stigmatosis coronatum; ovula in loculis 2, superposita. Valvulae 1-spermae, a rostro dehiscentes, caudis a basi ad apicem (sicut in genere Erodio) cochleiformiter revolutis. Semina exalbuminosa; embryonis radicula inter cotyledones convoluto-plicatas sita. — Herbae vel suffrutices, erecti vel decumbentes. Folia opposita vel alterna, crenato-dentata vel dissecta, semper

stipulata. Pedunculi axillares, rarius pseudo-basales, bracteati, 2- vel umbellatim pluriflori, rarius abortu uniflori. Valvularum caudae aut intus ciliatae vel glabrescentes, aut plumosae."

De 29 soorten van het in hoofdzaak Afrikaanse geslacht worden in 7 secties gegroepeerd. Voor de Tilburgse planten voeren l.c. p. 291 de eigenschappen:

"B. Valvularum cauda intus pilis ciliaribus obsita.
  a. Corolla media magnitudine; petala integra vel—apice retuso—leviter emarginata.
    α. Calyx apertus, campanulatus.
      II Annuae. Folia oblongo-linearia vel oblonga."

tot Sect. 5 *Biflorae*. Deze sectie bestaat uit 3 soorten en men komt l.c. p. 304 door "Fructus maturus 3 cm longus. Lamina 17 mm longa et 6 mm lata" tot *M. brevirostrata*, die l.c. p. 306 als volgt beschreven wordt:

"Annua, suffruticosa, 10—20 cm alta. Radix usque 8 cm longa, satis tenuis, fusca. Caulis ascendens vel basi procumbens, e basi ramosus vel ramosissimus ramis ascendentibus, indumento brevi puberulo et pilis longis patulis sparsioribus obsitus, subteres, usque 2 mm crassus, dense foliatus. Foliarum lamina subtus ad venas pilosa, ceterum saepe glabrescens vel glabra, ambitu lanceolata, basi cuneata, apice obtusa, margine irregulariter serrato-erosa, plerumque 17 mm longa et 6 mm lata; petioli longitudine diversi, in eodem specimine saepe quam lamina 2-plo breviores et 1½-plo longiores, indumento brevissimo puberulo et pilis longis patulis sparsis obsiti, 5 –20 mm longi. Stipulae subulatae, pilosulae, usque 4 mm longae. Pedunculi 2-flori, tetrabracteati, 10—20 mm longi, puberuli; in eodem specimine non raro pedunculi uniflori bibracteati vel — pedunculo ipso nullo — ebracteati. Bracteae stipulis conformes, 2 mm longae. Pedicelli 7—8 mm longi puberuli et pilis patulis sparsissimis obsiti, recurvati, fructiferi saepe sub calyce erecti. Sepala lineari-lanceolata, margine membranacea, vix manifeste mucronata mucrone 1 mm longo, 6—7 mm longa, pubescentia. Petala integra, cuneato-obovata, calyce breviora vel summum eidem aequilonga, coerulescentia. Stigmata vix 1 mm longa. Fructus maturus 3 cm longus; valvulae hirsuto-pubescentes; rostrum brevissime puberulum.

Kaffraria: Zuurberge (Schlechter a. 1895 n. 6573!), Ost Griqualand: zwischen Elliot und Maclear um 1500 m (Bolus, Austro-afric. a. 1896 n. 8725 — Typus in Herb. Berol.!)".

Tot deze soort behoren de Tilburgse vondsten van 1938, 1947, 1948 en 1950. De soort wordt genoemd in The Adventive Flora of Tweedside by HAYWARD and DRUCE (1919) p. 49: "First British record: I.M.H. 1914. Found on shingle at the confluence of the Gala and the Tweed, Selkirk. Flowering August to September. Det. A. THELLUNG" en door LAWALREE: Notice sur des Phanérogames adventices en Belgique. Bull. Soc. Roy. de Bot. de Belgique (1950) p. 44: "Adventice au voisinage des industries lainières: Verviers, graviers de la Vesdre en deux endroits différents — VISÉ."

7. **Monsonia biflora** D. C. Prodr. 1 (1824) p. 638 = *M. angustifolia* E. Mey. De plant, die ik 18 Augustus 1941 te Tilburg verzamelde, verschilt van het *Monsonia* materiaal uit het vorige nummer door smallere bladen, langere en smallere, haast naaldvormige steunbladen, iets grotere bloemen, langere naaldjes aan de toppen der kelkbladen, langere stijlen, sterker klierachtige beharing en langere rijpe vruchten. De soort behoort eveneens tot de sectie *Biflorae* Kunth en men komt in de monografie l.c. p. 304 tot *M. biflora* door de eigenschappen: "Fructus maturus 5—7 cm longus. Lamina 2—3 cm longa et 4—5 mm lata. Corolla coerulescens vel albida."
De beschrijving luidt l.c. p. 305:
"Annua, suffruticosa, 15—40 cm alta. Radix satis brevis, 3—10 cm longa, pallide fusca. Caulis ± erectus vel ascendens, e basi ramosus vel ramosissimus ramis ascendentibus, indumento brevi puberulo et pilis longis patulis sparsioribus obsitus, subteres, 2—4 mm crassus, satis dense foliatus. Foliorum lamina pilosa pilis saepe glandulosis, ambitu lineari-oblonga, basi cuneata, apice obtusa, crenato-serratula, saepe 2—3 cm longa et 4—5 mm lata; petiolus quam lamina 1½—2½-plo brevior, indumento brevi puberulo et pilis longis patulis sparsioribus obsitus, 8—17 mm longus. Stipulae setaceae, pilosae, 5—10 mm longae. Pedunculi 2-flori, tetrabracteati, 5—15 (raro 25) mm longi, puberuli; in eodem specimine non raro etiam nonnulli pedunculi uniflori bibracteati, vel — pedunculo ipso nullo — ebracteati. Bracteae stipulis plane conformes. Pedicelli 2½ cm longi, crassiusculi, puberuli et pilis sparsis longis patulis obsiti, sub fructu saepissime recurvati. Sepala spathulato- vel lanceolato-oblonga, margine late membranacea, mucronata, mucrone 1—3 mm longo, 10—12 mm longa, subhirsuta. Petala integra, obovato-cuneata, quam calyx 1¼-plo longiora, coerulescentia vel albida. Stigmata 1—1¼ mm longa. Fructus maturus 5—7 cm longus; valvulae hirsuto-pubescentes; rostrum brevissime dense puberulum.
Ueber den gröszten Teil des südlichen und mittleren Afrika, im Osten vom Kapland bis Eritrea, im Westen bis Angola verbreitet. Zumeist an dürren Stellen auf Sandboden. Bei den Buren unter dem Namen Slangebos gegen Schlangenbiss und Dysenterie bei Menschen und Vieh gebraucht. Blühend und fruchtend Dezember bis März."
Probst geeft in Wolladventivflora Mitteleuropa's (1949) p. 120 de vindplaatsen: "Derendingen 1917 (!); Döhren 1917, 18 (Scheuermann); Leipzig 1934, 36, 38 (Fiedler); Spinnerei Cossmannsdorf 1937 (Stiefelhagen); Hetzheide u. Luckenwald 1933 (Brandes, Bernau); England (Druce Plant list II) wo? (!) ob wolladventiv? (!); Lackalänga 1924, 25, 32, 34 (C. Blom)."

8. **Acer pseudo-platanus** L. f. **complicatum** Mortensen (door S. J. van Ooststroom). Fig. 1.
Deze in de bouw van de vrucht afwijkende vorm werd aangetroffen in een tweetal exemplaren in het Linschoter bos bij Linschoten, in November en December 1950, door E. E. van der Voo (H.L.B. 950. 348—545). Volgens de boswachter betreft het twee c. 20 jaar oude

bomen, die daar ter plaatse opgeschoten zijn samen met normale exemplaren.

In tegenstelling tot de meestal hier voorkomende individuen der soort, die vruchten hebben, waarvan de vleugels uiteenwijken en elkaar niet bedekken, hebben de vruchten van de f. *complicatum* vrijwel evenwijdige buitenranden, terwijl de vleugels over elkaar heen grijpen (fig. 1).

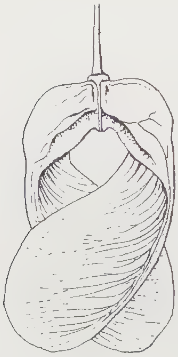

Fig. 1. *Acer pseudo-platanus* L. f. *complicatum* Mortensen, vrucht.

De f. *complicatum* Mortensen werd beschreven in Bot. Tidsskr. ser. 3, vol. 2, 1878, p. 253: "med rødlige, over hinanden sammenfoldede Frugtvinger". Pax in zijn monografie der *Aceraceae* in Pflanzenreich IV, 163 (1902) p. 20 schrijft: "alae subparallelae sese invicem tegentes". Een verhandeling over de variabiliteit der vruchten vindt men bij Vogler in Jahrb. St. Gallischen Naturw. Ges. 1906 (1907) p. 333—366. Hierin wordt ook een vrucht afgebeeld, die geheel overeenkomt met die van f. *complicatum* (plaat 2, fig. 10). Vogler komt tot het resultaat, dat de variabiliteit in vruchtvorm wat betreft de hoek, die de vleugels maken en de grootte der vleugels van weinig systematische waarde is. Wel van waarde is waarschijnlijk de vorm van de vleugels.

9. **Angelica sylvestris** L. var. **vulgaris** Avé-Lallemant f. **incisa** (Aschers.) Thell. (door S. J. van Ooststroom).

Deze vorm, die waarschijnlijk van weinig systematische waarde is, werd gevonden door de heer E. E. van der Voo, Woerden, op 16 Augustus 1950, aan de Brededijk te Papekop (Z.H.), (herb. Van der Voo). Zij is gekenmerkt door de onregelmatig en diep ingesneden blaadjes. Thellung in zijn fraaie en uitvoerige bewerking der *Umbelliferae* in Hegi, Ill. Flora von Mittel-Europa V, 2, schrijft op p. 1335: "Diese Form entsteht, wie schon Wimmer und Grabowski (Flora Silesiaca I, 1827, p. 264) mit Recht bemerken, vorzugsweise als Verstümmelungsform an den Ersatztrieben solcher Stöcke, deren Haupttrieb frühzeitig durch Mähd oder eine andere Ursache zerstört worden ist, und findet sich infolgedessen zuweilen auf dem gleichen Stock mit den normalen Blättern des stehengebliebenen Stumpfes des Haupttriebes." Dit laatste was bij de door Van der Voo gevonden plant ook het geval. Zijn herbarium bevat naast bladen van de afwijkende vorm der f. *incisa* ook bloeiende stengels met normale bladen, volgens zijn opgave van dezelfde plant afkomstig.

10. **Trigonella.**

Naar aanleiding van mijn vondst van de eerste woladventieve *Trigonella* in Nederland op 11 Augustus 1950 bij de Tilburgse Wolwasserij hebben Dr S. J. VAN OOSTSTROOM en ik, aan de hand van G. ŠIRJAEV: Generis *Trigonella* L. revisio critica in Publications de la Faculté des sciences de l'université Masaryk (1928—1934) en het buitenlandse materiaal in het Rijksherbarium te Leiden, al het Nederlandse *Trigonella* materiaal in ons beider herbaria nog eens doorgezien. Hierbij bleek, dat vooral de nomenclatuur nog al wat te wensen overlaat. ŠIRJAEV verdeelt de 74 soorten van het geslacht over 15 Sectiones samengevat in 3 Subgenera.
Subgenus I. *Trigonella* Beck emend; l.c. I (1928) p. 11.
"Calix campanulatus v. rarissime subtubulosus, semper breviter pilosus v. glaber, legumina formae diversae, sed nunquam inflata."
Subgenus II. *Trifoliastrum* Beck; l.c. I (1928) p. 14.
"Calix campanulatus, breviter pilosus, legumina inflata, breviter rostrata erecta."
Subgenus III. *Foenum Graecum* Širjaev l.c. p. 14.
"Calix tubulosus et longe pilosus, legumina compressa v. teretia, linearia v. oblonga rostrata."
Van het Nederlandse materiaal komen in aanmerking: van Subgenus I, Sectio VI *Falcatulae* Boiss.; l.c. p. 12.
"Annuae; stipulae inferiores dentatae v. incisae, flores nutantes, calix campanulatus, legumina deflexa fere erostrata ± compressa, v. rarius teretia, linearia usque ovato-oblonga, suturis bene elevatis, semina levia v. tuberculata."

> Subsectio A. *Leves* Šir. "Flores plerumque minimi, legumina linearia usque ovato-oblonga, ± compressa v. ± teretia, nervis obliquis, longitudinalibus v. transversis, nec parallelis, semina levia."
>
> > Series 1. *Hamosae* Šir. l.c. p. 42. "Stipulae semisagittatae dentatae, flores in racemis capitulatis, pedunculi elevati, legumina linearia subcompressa, 6—16 mm longa nervis transversalibus et obliquis anastomosantibus ornata."

Hiertoe, met de beschrijving l.c. p. 43, de soort:
T. hamosa L. Annua; caules crassiusculi, elongati 30—60 cm l., procumbentes, glabri tantum in parte superiore sparse pilosiusculi; stipulae dentatae; foliola obovato-v. obovato-oblongo-cuneata, acute denticulata, retusa v. truncata, superne glabra subtus sparse appresse pilosiuscula, (3) 12—15 (20) × (2,5) 5—6 (8) mm; pedunculi pilosuli, aristati, (0,6) 1,5—4 cm l., folio aequilongi; racemus capitatus 0,5—1 × 0,5—1 cm, (3) 6—18-florus; pedicelli 1,5 mm l., pilosiusculi; calix ca 1,5 × 2 mm l., corolla 2—3-plo brevior, sparse pilosiusculus fere subglaber, dentibus triangularibus fere glabris tubo duplo brevioribus; corolla (3) 4—5 mm l., flava, vexillum obovato-emarginatum alis aequilongum, carina alis brevior, alae auricula brevi

instructae; legumen (6) 7—10 (12) × 1,75—2 mm, subteres lineare, obtusum mucronatum, subglabrum v. glabrum, plerumque semicirculariter curvatum interdum rectum, nervis incrassatis transversalibus et obliquis anastomosantibus ornatum; semen 1,5 mm l., leve, ovatum, 9—15-spermum."

Het materiaal Rotterdam 1 en 6 September 1922 leg. JANSEN en WACHTER in herb. pr. H.L.B. 924. 360—72 et 78; id. in herb. KLOOS; behoort wel tot var. *typica* Šir. l.c. p. 43: "Foliola plerumque 12—15 (20) mm longa, pedunculus 1,5—4 cm longus, capitula 6—18-flora, calix 2 et corolla 4—5 mm longi, legumina plerumque semicirculariter curvata, 7—10 (12) mm longa."

De soort hoort thuis in Egypte en Nubië (afwijkende vormen ook in Arabië en in O. Afrika) en is adventief ook gevonden in Engeland en Frankrijk.

In zijn literatuurlijst onder *T. hamosa* citeert ŠIRJAEV ook GAMS in HEGI Mitt. Fl. IV. 3. 1229 (1925), waarin de vindplaatsen Hamburg en Mannheim genoemd worden [de eerste ook in ASCH. & GRAEBN. Syn. VI. II (1907) p. 389]. Hij heeft echter geen Duits materiaal gezien.

Tot Subsectio B. *Tuberculatae* Šir. l.c. II (1929) p. 7. "Annuae; racemi pedunculati capitati; flores mediocres, legumina compressa transverse eleganter nervosa, nervis parce anastomosant., semina tuberculata," behoort

T. corniculata L., waarvan de beschrijving l.c. luidt:

"Annua; caules erecti v. ascendentes v. procumb., crassiusculi fere glabri tantum pilis sparsissimis hic inde praecipue in parte super. obsiti, usque ad 55 cm elatis; stip. denticulatae (superiores integrae) v. lacin.; foliola formae valde variantis: obovato- usque oblongo-cun., super.-lanc.-lin., omnia plerumque a medio acute denticulata, obtusa v. retusa v. truncata, inferiora plerumque 1—3 (4) cm × 8—12 (35) mm, superne glabra subtus tantum ad nervum med. sparsissime appresse pilosiusc.; pedunc. folio 2—4-plo long., (1,5) 3—6 cm l. tenues; racem. capitul. *ovato-oblong.* 8—15-fl.; pedic. tenues ca 3 mm l.; calix 3 mm longus glaber v. inter dentes pilis sparsis obsitus corolla 3-plo brevior, dentibus triangul. tubo brevioribus; corol. 6—7 mm l. lutea, vexillum obovatum profunde emargin. carina brevius, alae carina vexilloque breviores; legumen compressum glabrum lineare ± curvatum *acutum* 10—16 × (1,5) 2—3 mm, nervis transvers. tenuibus non anastom. ornatum; semen oblong. tubercul. hilo emarginatum."

Van deze soort, waarvan het hoofdverspreidingsgebied in Italië, Zuid-Slavië, Albanië en Griekenland ligt, maar die ook in Spanje, Frankrijk, Zwitserland en Duitsland gevonden is, liggen in het herb. van KOK ANKERSMIT exemplaren van Deventer (proeftuin) 1872 en Hort. Marocco 1880, vermoedelijk beide culta. Mogelijk behoort ook een ex. Amsterdam 1907 leg. G. H. H. ZANDVOORT in herb. HENRARD, H.L.B. 921. 260—1176 tot deze soort; daar vruchten ontbreken is dit echter niet uit te maken, bovendien lijken mij de stelen der bloeiwijzen te kort en de stipulae te groot.

Sectio XII. *Bucerates* Boiss. emend.; l.c. III (1930) p. 12 "Annuae, stip. saltem foliorum infer. basi dentatae v. incisae, flores leguminaque stricti (exc. *T. Monspeliaca*!) sessiles v. in racemis umbellatis v. subracemosis pedunculatis, corol. typi medicaginoidei flava v. aurantiaca, legum. linearia teretia v. subcompressa, reticulata v. rarius transversaliter nervosa v. rugosa, sutura utraque incrassata, semina cylindrica tuberculata rarissime leviuscula."

Subsectio A. *Erectae* Šir. l.c. p. 13 "Legumina erecta".

Series IV Sessiles Šir. l.c. IV (1931) p. 1. "Flores 1—5 (8) in angulo foliorum "sessiles", legumina ± curvata, saepe longa, reticulato-nervosa."

T. monantha C. A. Meyer. "Annua; caules procumbentes 5—30 cm. l., ramosi rarius simplices, adpressiuscule pilosi; stipulae semisagittatae basi denticulatae; foliola *obovata, oblonga v. elliptica basi clinoidea*, acute denticulata v. inciso-dentata usque pinnatifida, utrinque ± densiuscule pilosa, plerumque 5—10 × 4—5 mm; flores *solitarii v. rarius bini* pedunculo subnullo v. rarius usque 5 mm longo; bract. subulatae; calix 5 (6) mm l., dentibus *subulatis* tubo aequilongis pilosis, corolla parte tertia brevioribus; corolla flava 7—7,5 mm l. vexillo obovato, carina alisque *manifeste breviore;* legum. linearia plerumque 6—7 cm longa subcompressa subrecta v. saepius arcuata, erecta, adpresse densiusculo pilosa, *areolis angustissimis subcontiguis longitudinalibus* ornata."

var. **genuina** Šir. l.c. p. 4 "Legumina apice non hamata."

f. **integrata** Gdr. "Foliola denticulata."

Hiertoe behoort een ex. Erp 16 Juni 1938 leg. B. en TH. REICHGELT. herb. KLOOS.

f. **pinnatifida** Thell. "Foliola inciso-dentata v. pinnatifida." Hiertoe behoort Oostzaner Gat October 1932. leg. J. SCHOUTE, herb. KLOOS. Zie Ned. Kruidk. Arch. 43 (1933) p. 350.

var. **macroglochin** (Dur.) Šir. "Legumina apice hamata."

= *T. macroglochin* Durieu de Maisonneuve.

Hiertoe een ex. Erp 16 Juni 1938 leg. B. en TH. REICHGELT. herb. KLOOS. Zie Ned. Kruidk. Arch. 49 (1939) p. 187.

Een ex. in herb. Ned. Bot. Ver. en een in herb. KLOOS culta 1942 uit een plant leg. JOH. JANSEN en TH. REICHGELT Erp. 5 September 1941, die intermediair is tussen de beide genoemde variëteiten schijnt het best te etiketteren als:

T. monantha C. A. Mey. ad var. **macroglochin** (Dur.) Šir. vergens.

T. incisa Benth. De beschrijving bij Širjaev l.c. p. 11 luidt: "*T. monanthae, T. Noeanae et T. geminiflorae valde affinis, sed pedunculis fructiferis (pedunculi florif. abbreviati!) usque ad* 5—10 *mm longis* (1) 2—3-*fl. et maturis leguminibus non raro rectis compressis et plerumque latioribus (usque ad* 3 *mm), areolis pentaginis v. quadratis (diam.* 1 : 1)."

Deze soort verzamelde ik 2 September 1916 bij Deventer; 10 Augustus 1923 id. en 11 Augustus 1950 bij Tilburg.

T. polycerata L. De beschrijving bij Širjaev l.c. p. 12 luidt:

"Annua; caules prostrati v. ascendentes v. erecti, a basi ramosi v. rarius simplices, 25—45 cm l., adpresse ± pilosi; stipulae semisagitt. basi dentatae; foliola ovata v. subrotundata v. obovato-clinoidea, integra acute denticulata v. pinnatifida, 5—10 (13) × 5—7 (10) mm, utrinque sparse rarius dense pilosa; pedunc. subnulli brevissimi; flores 1—6 (8); bract. subulatae; pedic. subnulli; calix 3—4 mm l. dentibus subulatis pilosis tubo brevioribus, corolla parte quinta brevioribus; corolla flava 5 mm l.; vexil. obovatum subemarginatum; carina vexillo paulo brevior et alis paulo longior; stigma capitatum; legum. fasciculata 2—5 cm longa, linearia subcompressa semiarcuata multo rarius recta, adpresse pilosa, areolis fere aequilatis (diam. 1 : 1) ornata; semina oblongo-cylindr. ad hilum emarginata, tuberculata flava v. badia.

f. **vulgaris** Lge. Ascendentes v. prostratae ramis longiusculis, foliola mediocra, umbella 2—5-flora."

Hiertoe behoort een ex. leg. B. en Th. Reichgelt Erp 16 Juni 1938 in herb. Kloos. Zie Ned. Kruidk. Arch. 49 (1939) p. 185.

T. orthoceras Kar. et Kir. De beschrijving l.c. p. 16 luidt: "*T. polyceratae valde affinis, sed caule plerumque humiliore et glabriore, floribus 1—4, dentibus calic. tubo aequilongis, legumine tantum 2—3 cm longo, areolis longitudinaliter elongatis oblongis (diam. 2—3 : 1) aequilatis differt.*"

Hiertoe het ex. leg. Struykenkamp Buitenplaats Groenhoven bij Leiden Juli 1898 in herb. N.B.V., afgebeeld in Flora Batava en geciteerd in Širjaev l.c. p. 18.

Subsectio B. *Reflexae* Šir. l.c. p. 20 "Legumina sessilia reflexa"

T. monspeliaca L. Door Širjaev l.c. beschreven: "Annua; caules diffusi prostrati ramosi, adpresse densiuscule pilosi, ramis simplicibus erectis 3—35 cm longis; stipulae semisagitt. parvulae, inferiores incisae; foliola obovato-clinoidea superne acute denticulata, 4 —10 × 3—7 mm, utrinque adpressiuscule pilosa (foliola fol. inf. angustiora); pedunc. subnulli spina molli instructi; capitulae *4 —14-fl. sessiles*; bract. lineari-subulatae; pedic. brevissimi; calix 3 mm l., dentibus lineari-subulatis pilosis tubo longioribus, corolla parte quinta brevioribus; corol. flava 4 mm l.; vexil. obovato-elong. leviter emarginatum; alae carina paulo breviores auricula deorsum directa instructae; legum. *stellatim disposita linearia 7—13 (17) × 1—1,5 mm paulo compressa* paulo curvata pilosa v. rarius glabra *nervis transversalibus obliquis vix anastomosantibus valde incrassatis insculpta*, semina tenuiter tuberculata, 1,5 mm longa."

f. **typica** Eig "Foliola integra, leg. ovariumque adpresse pilosa", l.c. p. 24.

Hiertoe behoort het materiaal leg. Kloos. Wormerveer 24 Augustus 1925 in herb. pr.

f. **petiolata** (Post pr. var.) Šir. "Petioli foliis multo longiores 3—4 cm longi", l.c.

Hiertoe het ex. leg. Kloos. Weert 13 Augustus 1920 in herb. pr. Zie Ned. Kruidk. Arch. 1921 (1922) p. 90.

Subgenus II *Trifoliastrum* Beck. omvat alleen

Sectio XIV *Capitatae* Boiss. emend., bij Širjaev l.c. V (1932) p. 1.

Sectio XIII genoemd (drukfout) en als volgt beschreven: "Annuae, stipulae dentatae v. superiores integrae, pedicelli semper stricti rarius inferiores (fructiferi) recurvati, racemi pedunculati dense capitati, calix campanulatus, corolla coerulea typi simplicis, legumina teretia v. parum compressa, parva (3—6,5 mm longa), breviter et tenuiter rostrata, 1—2 (3) sperma, semina ovata tenuiter tuberculata v. laevia."

T. coerulea Ser. Širjaev geeft l.c. p. 4 de volgende beschrijving: "Annua; caules *erecti* simplices v. ramosi *ramis strictis*, fistulosi, plerumque (2) 3—6 (10) dm elati, sparse pilosi; stipulae triangulari-lanceolatae dentatae; folia ternata foliolis ovatis leviter retusis denticulatis 2—5 × 1—2 cm, foliolis folior. superiorum angustioribus *oblongis* 1,8—4,5 × 0,6—1,2 cm; pedunculi folio longiores, racemi florif. densissimi capitulaeformes *globosi* multiflori, *post anthesin paulo elongati*; pedicelli ca. 1 mm l., subrecti pilosi; calix 3 mm l., corolla 2-plo brevior, dentibus lanceolatis tubo subaequilongis; corolla 5,5—6,5 mm l., coerulea, vexillum oblongum emarginatum alis longius; legumina rhomboidea obovata inflata vix subcompressa 4,5 × 3 mm *in rostrum fere rectum ca. 2 mm longum satis repente abeuntia, cum rostro tubum calicinum triplo superantia* 1—2 (3)-sperma, legumina inferiora non raro recurvata; semina 2 mm longa obovata brunnea minutissime tuberculata."

Deze soort komt zeer zeldzaam en alleen uit kultuur in Nederlandse herbaria voor.

T. besseriana Ser. Hiervan zegt Širjaev l.c. p. 10: "*Differt a praecedente caulibus plerumque ascendentibus v. subrectis, a basi ramosis* (*ramis ascendentibus* ± *caulibus aequilongis*), *foliolis fol. angustioribus* (*folior. super. oblongo-lanceolatis usque linearibus*, 12—28 × 3—8 *mm*), *racemis florif. subglobosis v. ovatis usque* 30-*floris, post anthesin valde elongatis oblongis laxiusculis, leguminibus tubum calic.* 4-*plo superantibus in rostrum sensim attenuatis, nervis crassioribus ornatis.*"

Dit is de soort, die in Nederland en elders in West-Europa heel vaak als graan-adventief gevonden wordt en onder de namen *Melilotus coeruleus* Desr.; *Trigonella coerulea* Ser.; *T. coerulea* var. *procumbens* Spr.; *T. coerulea* ssp. *procumbens* Thell.; *T. procumbens* Rchb. in onze flora's wordt aangetroffen.

Deze soort is zeer variabel. Soms komen exemplaren vòor, die zeer veel op de echte *T. coerulea* Ser. gelijken, maar blijkens de harde, niet samendrukbare stengel en de geleidelijk in de snavel overgaande vrucht toch tot *T. besseriana* Ser. behoren. Daartegenover staat een exemplaar in herb. LAKO (H.L.B. No. 927. 10—112) leg. A. WALRAVEN bij Sluiskil 1853, dat men, determinerende volgens de Clavis dichotomica specierum van ŠIRJAEV l.c. VI (1933) p. 1 geneigd zou zijn te houden voor: **T. capitata** Boiss., maar dat toch aan de beschrijving dezer soort l.c. V (1932) p. 16 in verschillende opzichten (beharing, vruchtvorm) slecht voldoet.

Subgenus III *Foenum Graecum* Širjaev omvat alleen

Sectio XV *Foenum Graecum* Ser. bij Širjaev l.c. V (1932) p. 17 Sectio XIV (drukfout) genoemd en als volgt beschreven:

"Annuae, stipulae integrae rarissime dentatae, flores rarissime bracteolati, typi simplicis (alae sine dente conjunctivo), solitarii v. bini (usque 4) sessiles (i.e. racemus 1—2 (4)-florus apedunculatus), rarissime plurimi et in capitulum pedunculatum congesti, albo-ochroleuci, violascentes v. coerulei, plerumque magni, vexillo semper fere oblongo, sua latitudine triplo-multiplo longiore, calix *tubulosus pilis longis v. longissimis simplicibus obsitus, carina alisque usque duplo brevior*, legumina plerumque linearia rarius lanceolata, subcompressa v. teretia, saepe magna, recta v. ± curvata, plerumque longe rostrata, suturis ambis incrassatis, nervis longitudinalibus v. subobliquis ornata, 4—20-seminifera, semina magna ovata v. quadrata, tenuiter tuberculata v. levia."

Subsectio B. *Gladiatae* Boiss. l.c. p. 22.

"Flores *ebracteolatae sessiles solitarii v. bini* (usque 4), i.e. racemus sessilis 1—4-florus, legumen 4—5 cm una cum rostro longo longum nervis longitudinalibus ornatum."

Series 1. *Compressae* Šir. "Legumen compressum."

T. gladiata Stev. "*Annua*; caules *diffusi procumbentes raro erecti, plerumque* 5—25 *cm longi*, rotundi, dense pubescentes; stipulae parvae semiconnatae integrae pilosae; foliola foliorum obovato- usque ad lanceolato-clinoidea retusa apice acriter denticulata, plerumque utrinque sparse pilosa, 5—12 × 3—6 mm; flores *subsolitarii*; bracteae nullae; calix 6 mm l., longe patule pilosus, corolla sesqui brevior, dentibus lanceolatis plumoso-pilosia tubo subaequilongis; corolla 8—10 mm l., pallide ochroleuca, vexillo obovato-oblongo violaceo-suffuso stricto plano paulo emarginato, nervo centrali cum eodem laterali nervulo obliquo conjuncto, alis in parte tertia longiore, carina alis in parte tertia breviore antice non angulata apice rotundata, alis oblongis; legumina recta v. ± curvata, late lineari *compressa stricta* (*1,5*) *2—3* (*4*) *cm* × (*3*) *4—5* (*7*) *mm* (*sine rostro*) *in rostrum subaequilongum* 1—2 *cm longum rectum abruptiuscule angustata, pilosa, suturis nervis longitudinalibus prominulis anastomosantibus ornatis, 5—7-sperma*; semina ovata *ca 3,5 mm longa crebre denticulata*."

Hiertoe behoren: Rotterdam 6 September 1922 leg. JANSEN en WACHTER in herb. KLOOS. id. 27 September 1922 leg. J. en W. in herb. pr. H.L.B. No. 924. 360—87 en id. H.L.B. 924. 360—93. Middelburg leg. J. MESU en C. BRAKMAN.

var. **heterophylla** VAN Ooststr. et Kloos **nov. var.** *differt foliolis foliorum inferiorum pinnatifidis, superiorum ut in f. typica.*

Wormerveer 1 September 1932 leg. KLOOS in herb. pr.

Al deze vondsten in Nederland van de soort *T. gladiata* zijn graanadventieven.

Series 2. *Teretes* Šir. l.c. V (1932) p. 28 "Legumina teretia."

T. foenum-graecum L. "Annua, caules *erecti v. rarius procumbentes* 10—50 cm l. rotundi *cavi* ± ramosi, ramis strictis; stipulae integrae ovatae acuminatae ± pilosae; foliola foliorum ovata usque ad oblonga-lanceolata plerumque 2—3 (5) × 1—1,5 cm, in parte superiore denticulata; flores 1—2 in angulo foliorum subsessiles; calix 8 mm longus tubulatus ± pilosus, corolla duplo brevior, dentibus

lanceolato-linearibus longe pilosis tubo aequilongis; corolla *flavo-alba 13—18 mm l.*; ad basin violaceo suffusa, vexillo valde emarginato oblongo, in parte inferiore plica instructo, alis in parte tertia longiore, carina alis duplo breviore, alis *angulo excedente ornatis* carina duplo longioribus; legumina linearia ± curvata (*6*) *7—10* (*11*) × *0,4—0,5 cm* (*sine rostro*), *longitudinaliter nervis remotis anastomosantibus striata, in rostrum rectum* (*1*) *2—2,5 cm longum,* (*parte seminifera 3—5-plo brevius*) *sensim attenuata, 10—20-sperma glabra v.* ± *pilosa, sed demum glabrescentia*; semina 5 × 3 mm tenuiter tuberculata (sub oculo armato) badia v. flavo-badia."
Het merendeel der in herb. aanwezige exemplaren bestaat uit gekweekte exemplaren, alleen het ex. Gorinchem Juli 1912 leg. J. TH. HENRARD in herb. pr. H.L.B. No. 921. 260—1178 is een graan-adventief.

11. **Trifolium campestre** Schreb. f. **verticillatum** Van Ooststr., nova forma (door S. J. VAN OOSTSTROOM).
Zowel bij *Trifolium dubium* Sibth. als bij *Medicago lupulina* L. vindt men behalve exemplaren met de normale, in de bladoksels der verspreide bladen staande hoofdjes, ook soms planten waarbij aan het einde van de takken de hoofdjes kransvormig of schermvormig opeengehoopt zijn. Dit komt voor bij *Trifolium dubium* Sibth. f. *umbellatum* (Knaf) Van Ooststr. (*Trifolium filiforme* L. var. *umbellatum* Knaf in Čelak., Prodr. Fl. Böhm., 1867, p. 662) en bij *Medicago lupulina* L. f. *polystachya* Ser., pro var. Voor zover ik uit de literatuur kan nagaan was de parallel-vorm hiervan bij *T. campestre* nog niet bekend. Een exemplaar, dat als zodanig te beschouwen is werd mij toegezonden door de Heer H. M. HEYBROEK te Wageningen, die het vond in Midden-Limburg aan de linker Maasoever, tegenover de mond van de Swalm, op 5 Juni 1949. Deze f. *verticillatum* bevindt zich in het Rijksherbarium, no. 949, 180—202 en onderscheidt zich als volgt: capitula verticillata, in axillis foliorum superiorum verticillatorum.

12. **Trifolium glomeratum** L. var. **minus** Rouy, Fl. de Fr. V (1899) p. 88. Tezamen met prachtig materiaal van *T. tomentosum* L. (vroeger in ons land waargenomen: Apeldoorn 1877 KOK–ANKERSMIT; Herzogenrath 1914 DE WEVER; Tilburg 1947 KLOOS) en *T. glomeratum* L. (bekend van Apeldoorn 1877 KOK–ANKERSMIT; Tilburg 1938 PATER LUDOVICUS en K; 1939 K; 1940 K steeds in de normale typische vorm) vond ik op 11 Augustus 1950 te Tilburg bij een wol- en huidenfabriek enkele exemplaren van de var. *minus* Rouy, waarvan de beschrijving l.c. luidt:
"*minus* Nob.; *T. Perreymondi* Bot. Gall. occid. nonnull. — Capitules d'un tiers plus petits que dans le type; la plupart subsessiles; étendard un peu plus court, obové; port du *T. cernuum* Brot. çà et là, souvent avec le type: Gironde, Aude, Puy-de-Dôme, Maine-et-Loire, Seine-et-Oise."
ASCHERSON und GRAEBNER geven in Syn. M. E. Fl. VI. 2 (1910) p. 509 een beschrijving van de var., die een vertaling van die van ROUY is en laten daarop volgen: "So in Frankreich mehrfach, ob auch bei uns?"

Hegi in Ill. Fl. M. Eu. IV. 3 (1924) p. 1279: "im Hafen von Mannheim und in Karlsruhe 1910."
De Tilburgse exemplaren onderscheiden zich van de type, behalve door de bovengenoemde kenmerken nog door dunnere stengels en kleinere blaadjes, zodat de gehele plant een meer tengere en sierlijke indruk maakt.

13. **Dorycnium hirsutum** (L.) Ser. var. **incanum** Ser. ap. DC. Prodr. 2 (1825) p. 208.
Lotus hirsutus L. var. *incanus* Lois. = *Bonjeania hirsuta* Rchb. var. *incana* Koch behoort tot het ondergeslacht *Bonjeania* (Reich.) Boiss. waarvan de beschrijving bij Rouy Fl. de Fr. V (1899) p. 132 luidt: "Calice 5-partit, à divisions ascendantes plus ou moins inégales. Pétales libres; étendard oblong-cunéiforme, atténué en un large onglet canaliculé; ailes connées en avant, plus longues et plus larges que la carène droite, obtuse. Style ascendant; stigmate capité. Légume droit, exsert, pleiosperme, déhiscent, enflé à la maturité; graines séparées par du tissu cellulaire. Plantes suffrutescentes; feuilles courtement pétiolées; capitules axillaires, pédonculés, involucrés." De dan volgende beschrijving van de soort luidt: "Plante buissonnante de 2—5 décimètres, velue, très rarement presque glabre. Tiges couchées, ascendantes ou redressées, rameuses, à rameaux arrondis. Folioles oblongues-cunéiformes; aigues ou obtusiuscules-mucronées. Stipules ovales ou lancéolées, bien plus longues que le pétiole très court. Capitules grands 5—10-flores; pédoncule plus long que la feuille. Calice subbilabié, très velu, à divisions une fois plus longues que le tube, les inférieures plus longues que les autres. Corolle une fois plus longue que le calice; étendard et ailes d'un blanc plus ou moins teinté ou strié de rose; carène d'un pourpre noir. Légume ovoide ou presque oblong, noirâtre, inégal, glabre, à valves non tordues à la maturité. Graines subglobuleuses. — Mai-juillet." De var. wordt dan l.c. p. 134 beschreven als: "Une forme: *B. incana* Rouy. Plante plus trapue, plus robuste; folioles épaisses, blanches tomenteuses et feutrées-soyeuses; pétioles moins courts; capitules courtement pédonculés, plus multiflores, légumes plus gros. Hab. Littoral des Alpes-Maritimes et de la Provence, de Nice à Toulon."
Ik kreeg de plant ter determinatie toegezonden door de Heer C. J. v. d. Vegt, die haar in October 1950 vond in een *Berberis*struik in het gemeentelijk plantsoen aan de Laan van Meerdervoort in Den Haag. Het vermoeden lag voor de hand, dat het een verwilderde sierplant zou zijn. Op mijn verzoek om eventuele inlichtingen aan de Heer Doorenbos, Directeur der Gemeentelijke Plantsoendienst, was deze zo vriendelijk mij te schrijven: "± 15 jaar geleden heb ik 25 of 50 *Dorycnium* gekocht van de firma J. Hoogendoorn te Boskoop. Deze planten waren geïmporteerd uit Frankrijk. Echter is gebleken, dat ze niet winterhard waren. Zeer waarschijnlijk heeft een zaailing op een gunstig beschut plekje zich weten te handhaven."

14. **Coronilla varia** L. met abnormale bloeiwijze (door S. J. van Ooststroom).

In het herbarium van de Heer A. G. de Wilde, Leiden, bevindt zich een plant van *Coronilla varia* L., waarbij de as van de bloeiwijze aan de top doorgegroeid is en daar bladen draagt. Het exemplaar werd gevonden door de Heer De Wilde op een terrein aan de Rijnsburgerweg te Leiden op 14 November 1948, tussen vele normale planten. Een dergelijke afwijking wordt vermeld door Penzig, Pflanzenteratologie, 2. Aufl. II, 1921, p. 263 en door Gams in Hegi, Ill. Flora von Mittel-Europa IV, 3, 1924, p. 1475.

15. **Vicia grandiflora** Scop. var. **biebersteinii** Griseb. (door S. J. van Ooststroom). Fig. 2.

De var. *biebersteinii* Griseb. van *Vicia grandiflora* Scop. wordt het eerst voor Nederland vermeld van Middelburg door Kloos in N.K.A. 46, 1936, p. 460. Zij is gekenmerkt door de smalle, lijnvormige blaadjes der bovenste bladen, die tot 10—12 maal langer dan breed kunnen zijn. De blaadjes der onderste bladen zijn vaak breder. Een tweede exemplaar werd gevonden in een greppel langs een korenveld op het landgoed De Treek, ten N. van de straatweg Zeist–Woudenberg, door A. Eisses in Juni 1950. Deze plant heeft de blaadjes der bovenste bladen lijnvormig, terwijl hun van een priemvormig spitsje voorziene top uitgerand is en zijdelings twee oortjes vertoont; de blaadjes der onderste bladen worden geleidelijk breder en zijn langwerpig en geheel onderaan omgekeerd eirond, met uitgerande top en topspitsje (fig. 2). De bloemkroon van het door Kloos opgegeven exemplaar is kleiner dan bij de andere vormen van de soort; het exemplaar van Maarn vertoont de gewone, grote *V. grandiflora*-bloemen.

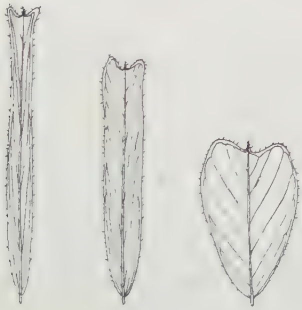

Fig. 2. *Vicia grandiflora* Scop. var. *biebersteinii* Griseb., van links naar rechts: blaadje van een der bovenste, middelste en onderste bladen.

16. **Cuscuta europaea** L. var. **conocarpa** Engelm. (door S. J. van Ooststroom). Fig. 3.

In mijn bewerking van het geslacht *Cuscuta* voor Nederland, in N.K.A. 52, 1942 wees ik erop (p. 179), dat Yuncker naast de typische vorm een tweetal variëteiten van *C. europaea* L. onderscheidt, nl. var. *indica* Engelm. en var. *conocarpa* Engelm. Deze laatste verschilt van typische exemplaren van de soort door het bezit van een kegel- of peervormige vrucht. Nu vond ik bij het doorwerken van het materiaal, dat aanwezig is in de diverse Nederlandse herbaria, meermalen exemplaren met min of meer duidelijk kegel- of peervormige vruchten, die ik dan ook beschouwde als tot var. *conocarpa* te behoren. Fig. 3b vertoont een deksel van een dergelijke vrucht, terwijl fig. 3a een meer bolvormige vrucht doet zien. Zoals uit de beide tekeningen duidelijk wordt, is het verschil maar gering. Ik meende dan ook, dat ik in het Nederlandse materiaal een onderscheiding van de var. *conocarpa* achterwege kon laten. Achteraf blijkt nu, dat er bij *C. europaea* exemplaren voorkomen, waarbij de vruchten veel duidelijker kegelvormig zijn. Deze zijn echter hier te lande beslist zeldzaam, daar ik bij het talrijke door mij indertijd onderzochte materiaal geen enkel exemplaar aantrof met een dergelijke vruchtvorm. Het eerste Nederlandse exemplaar, dat als echte var. *conocarpa* beschouwd kan worden, werd gevonden door Dr J. Brand, bij Bronkhorst, in N6.56.44, op 16 October 1950 (in herb. Kloos; H.L.B. 949. 328—9). Het deksel van een vrucht dezer plant is hierbij afgebeeld in fig. 3c. De var. *conocarpa* wordt door Yuncker in zijn monografie van het geslacht *Cuscuta* als volgt gekarakteriseerd: "Similar to *C. europaea*, with which it intergrades, differing, however, in having a markedly conic or pyriform capsule." Uit deze beschrijving en het onlangs gevonden materiaal blijkt, dat, wat ik vroeger (l.c. p. 179) als var. *conocarpa* beschouwde, een tussenvorm is tussen deze variëteit en de typische vorm van de soort.

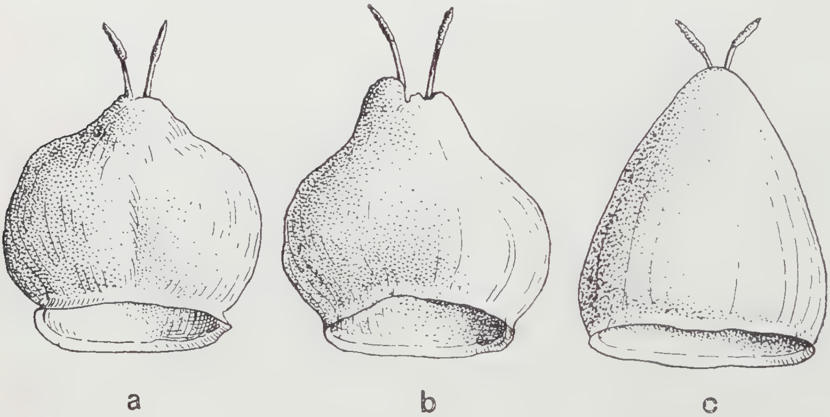

Fig. 3. *Cuscuta europaea* L., *a.* deksel van de vrucht der typische vorm; *b.* id. van een overgang naar var. *conocarpa*; *c.* id. van var. *conocarpa* Engelm.

17. **Datura quercifolia** H. B. K. Nov. Gen. & Sp. 3 (1818) p. 7. Fig. 4.

In Synopsis of the genus *Datura* van W. E. Safford (Journal of the Washington Academy of Sciences Vol. 11 No. 8 (1921) behoort deze soort tot de sectie *Stramonium* Gaertn. waarvan de beschrijving op p. 175 luidt:

"Flowers erect; calyx tube circumscissile near the base, falling off together with the corolla, the base persisting and expanding into a disc, the margin of which is at length turned downward and frilled. Corolla distinctly 5-lobed, the lobes separated by emarginate sinuses. Fruit an erect regularly dehiscent 4-valved capsule, armed with rigid spines or unarmed." De eigenschappen

"Capsule armed with *strongly unequal* spines, the upper ones longer and stouter.

Leaves *pinnately* lobed.

Branches, petioles, and calyx *downy or woolly*" voeren dan l.c. tot de soort, waarvan dan l.c. p. 177 nog gezegd wordt:

"Type locality: Crescit locis temperatis Regni Mexicani prope Zelaya et Molino de Saravia, alt. 930 hex."

Range: Texas to Arizona and Mexico.

A common weed along the banks of ditches. Leaves pinnately lobed; pericarps armed with large rigid ascending spines."

E. LUNDSTRÖM schrijft in een artikel: Plantae in Hort. Bot. Bergiano critice examinatae in Acta Horti Bergiani V, 3 (1914) p. 91:

"*D. quercifolia* Humb. & Bonpl. Diese charakteristische Art, die zuerst in Mexico von Humboldt und Bonpland entdeckt wurde, kann man kaum durch Samen aus den bot. Gärten erhalten, trotzdem dass sie in den Tauschkatalogen fleissig aufgenommen wird. Nur ein Garten scheint, wie oben erwähnt wurde, Samen der richtigen Art zu liefern (Montpellier). Die übrigen liefern zuweilen *D. Tatula*, zuweilen eine ziemlich niedrig wachsende dunkelblättrige *Datura*, die under dem Namen *D. Leichhardii* Muell. geht. *D. quercifolia* ist zu erkennen an ihrer ziemlich geringen Höhe 30—50 cm, ihren etwas an *Solanum Lycopersicum* L. erinnernden Blättern, ihren kleinen (etwa 5 cm tiefen) an Farbe denjenigen der *Bernhardii* ähnlichen Blumen und ihren sehr originellen mit sitzenbleibendem Kelch versehenen Kapseln deren langen, spitzen, oft wie Bogen gebeugten Stacheln an der Basis sehr breit und dazu stark zusammengedrückt sind. Die Exemplare dieser Art, die in H. B. kultiviert sind, sind alle, besonders an Zweigen, Blattstielen und Blattnerven und am Blumenkelch ausgespreizt langhaarig gewesen. Das Exemplar von PRINGLE an einem natürlichen Standort in Mexico eingesammelt, das im Naturhistorischen Reichsmuseum des Staates aufbewahrt ist, ist dagegen von viel kürzeren, mehr zugedrückten Haaren bekleidet.

Diagnosis. Caulis teres, ± villosus, 30—50 cm altus; folia ovata, sinuato-pinnatifida, similia *Solani lycopersici*, subtus praesertim ad nervos villosa; flores parvi, ca 5 cm, calyce duplo longiores, rubro-violacei; calyx quinquangulatus, viridis, ± dense villosus; capsula magna, calyce emarcido remanente, maxime inaequaliter aculeata, ca 7 cm longa, ca 5 cm lata, aculeis acutissimis, ad basin late compressis; semina compressa, reniformia, nigra, testa crustacea, *D. stramonii* similia.

In DE CANDOLLES Prodromus wird die Länge der Blumenkrone unrichtig angegeben. In Wirklichkeit ist sie zwei (nich drei) mal länger als der Kelch. Weiter werden die Zähne des Saums als besonders spitz angegeben — sie unterscheiden sich indessen nicht von den des *Stramonium*typus. Zuletzt wird die Blumenfarbe als blass violett bezeichnet — sie ist doch recht stark rotviolett."

In het begin van September 1950 stuurde de Heer G. ENGELS te Helden mij een bijna rijpe *Datura*-vrucht, die door Dr R. HEGNAUER, die veel *Datura*-soorten gekweekt heeft, als *D. quercifolia* herkend werd. Later zond de Heer ENGELS nog enkele overgebleven zijtakken met onrijpe vruchten. Hoewel de daaraan voorkomende bladen maar heel weinig op die van *Solanum lycopersicum* lijken, de plant afkomstig van een maïs-akker te Helden zeker groter was dan 50 cm en de bloemen waarschijnlijk wit waren (zij gelijken volgens de Heer ENGELS zeer veel op die van *Datura Stramonium*), lijkt mij de overeenkomst van de levende vrucht met de afbeelding bij het artikel van LUNDSTRÖM l.c. pl. IV zo frappant, dat aan de juistheid der determinatie van HEGNAUER wel geen twijfel kan bestaan.*) Vermoedelijk is *D. quercifolia* nog op een tweede vindplaats bij Helden, en wel in een akker met stambonen opgeslagen, maar zekerheid hieromtrent bestaat niet, daar deze planten voor de bloei zijn uitgeroeid. "Het lijkt mij waarschijnlijk, dat de zaden dezer plant zijn aangevoerd met gemengd graan voor kippen, waarin dikwijls maïs en granen van buitenlandse herkomst voorkomen", aldus de Heer ENGELS in litt.

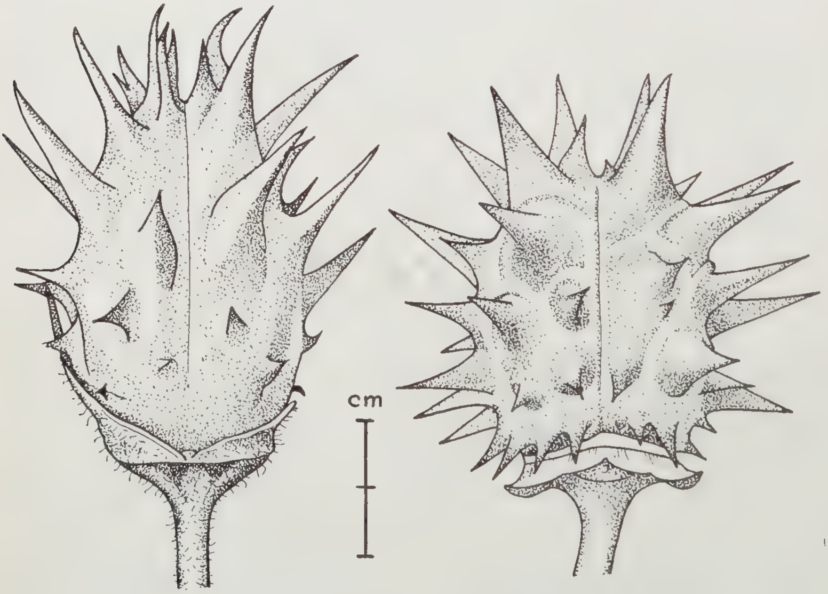

Fig. 4. Vruchten van *Datura quercifolia* (links) en *D. ferox* (rechts) naar de afbeeldingen van LUNDSTRÖM

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*) Nader onderzoek bracht HEGNAUER tot de overtuiging dat de gevonden plant *Datura ferox* L. is.

18. **Plagiobothrys australasicus** (DC.) Johnston = *Eritrichium australasicum* DC. (Prodr. X, 1846) p. 134 = *Allocarya australasica* (DC.) Greene, Erythea III (1895) p. 57. In zijn artikel II, Studies in the Boraginaceae in Contr. Gray Herb. of Harvard University New Series LXVIII (1923) geeft I. M. JOHNSTON onder 4. A synopsis and redefinition of the Genus *Plagiobothrys* p. 57, een breed opgezet, sterk gedocumenteerd betoog om het geslacht *Plagiobothrys*, dat oorspronkelijk bij FISCHER en MEYER monotypisch was, een veel wijdere betekenis te geven. Hij schrijft o.a. l.c. p. 62: "Because of the lack of consistently diagnostic characters which would separate them, *Allocarya*, *Echidiocarya*, and *Sonnea* are all merged with *Plagiobothrys*. The result is a genus which appears to be a very natural one, and one which admits of great precision in definition. The amplified *Plagiobothrys* is at once distinguished from its nearest relatives, *Cryptantha* and *Oreocarya*, by the lack of a pronounced longitudinal ventral groove, and the possession instead of a well-developed ventral keel and a definitely circumscribed small scar. The gynobase is a pyramid or low frustum and very much shorter than the nutlets, and is not subulate and about equalling the nutlets as in *Cryptantha* and *Oreocarya*. The nutlets in *Plagiobothrys* are commonly keeled and usually rugose, whereas in *Cryptantha* and *Oreocarya* they are rarely if ever keeled and the roughenings usually tuberculate or muricate. The pubescence in *Plagiobothrys* is mostly appressed and is less stiffly spreading than is the hispid indument characteristic of *Cryptantha*." "As a result of this study and with the hope that it will give the paper a wider usefulness I have included a rough key to the accepted species." In deze determinatietabel l.c. p. 64 voeren de eigenschappen:
"Leaves opposite at least below.
  Nutlets attached directly to gynobase, without a definite stipe-like ventral prolongation." tot § *Allocarya*, en dan

"Plants annual.
  Spikes solitary.
    Dorsal keel extending down length of nutlet, usually well-developed.
      Scar of nutlet solid, not below level of ventral keel; nutlets vitreous; Australian . . . . *P. australasicus*"

en l.c. p. 75: "This is the only extra-American species of the genus." In Contr. Gray Herb. of Harvard University LXXXI (1928) geeft JOHNSTON in Studies in the Boraginaceae onder 2. Notes on various Boraginoideae op p. 75 en 78 de beschrijvingen van *P. plurisepalus* (F. v. Muell.) Johnston = *Maccoya plurisepalea* F. v. Muell. = *Rochelia plurisepalea* Druce en van *P. elachanthus* (F. v. Muell.) Johnston = *Heliotropium elachanthum* F. v. Muell., twee australische soorten, die wel met *Eritrichium australasicum* verward zijn. Daarna volgt dan ter onderscheiding daarvan l.c. p. 79 de volgende beschrijving van "*Plagiobothrys australasicus* (DC.) Johnston: Annual; stems one to several, erect or prostrate, (including the inflorescence) 5—12 cm long, usually with several strictly ascending simple laterals from below the middle, sparsely strigose; leaves linear, 1—3 cm long, 1—2 (—2,8) mm broad, obtuse, spreading, glabrous or sparsely appressed short-hispid, lower ones opposite, margins ciliate and frequently pustulate; racemes 3—8 cm long, remotely flowered, interruptedly bracted, simple; calyx in flower ca. 1,5 mm long, appressed villous-hispid, divided into 5 erect lance-oblong lobes; fruiting calyx 2—2,5 mm long, the lobes lanceolate, herbaceous and ascending; pedicels thickened, ca. 0,5 mm long, ascending; corolla inconspicuous, white but drying brownish, ca. 1,8 mm long, shortly surpassing the calyx; limb 0,7—1 mm broad, with 5 ascending obovate lobes; stamens borne just below middle of tube; corolla-throat with 5 weekly intruded puberulent spots; ovules 4; nutlets 4, pale or fuscous, opaque, ca. 1,3 mm long, compressed-ovoid, angulate, roughened on the back and sides with loosely reticulate ridges that anastomose with the well developed medio-dorsal keel, ventral face with a large areola sunken below the crest of the keel, ventral keel extending down to about middle of the nutlet and paralleled and crowded on either side by wrinkles in the pericarp; areola inframedial, triangular, more or less excavated, about 2/5 length of nutlet, not oblique; gynobase pyramidal; style reaching to about 4/5 height of nutlets. Western Australia: Swan River 1839, DRUMMOND. —

This species is apparently restricted to Western Australia; the forms from eastern Australia passing as this species being in large part at least: *P. elachanthus*. It is evidently quite distinct from that species differing in its opaque, more compressed nutlets and very different nutlet-attachment. The areola is decidedly triangular and somewhat excavated and is located on the lower half of the nutlet evidently sunken below the level of the ventral keel. It appears to be rather closely related to *P. procumbens* (Colla) Gray of Chile."

Op 8 Juni 1950 verzamelde ik een 10-tal exemplaren van de soort te Tilburg bij een wol- en huidenfabriek.

In de jaren 1909—1916 is zij ook gevonden "in the moist alluvium near the junction of the Tweed and Gala, SELKIRK. An undoubted wool alien leg. miss I. M. HAYWARD, det. G. C. DRUCE." HAYWARD and DRUCE: The adventive Flora of Tweedside (1919) p. 161. Dit is de enige vondst vermeld in R. PROBST, Wolladventivflora Mitteleuropas (1949) p. 132.

19. **Chelone glabra** L. (door S. J. VAN OOSTSTROOM).

Deze soort werd op 27 Augustus 1950 gevonden door A. W. M. POLDERS op het landgoed Warnsborn bij Arnhem, volgens opgave van de vinder "aan de rand van een vrij zacht stromend water, in vermoedelijk *Alnion glutinosae*-verbond, met *Lycopus europaeus*, *Dryopteris thelypteris*, *Salix*, *Scutellaria galericulata*" (H.L.B. 950. 325—166). *Chelone glabra* is een soort van Noord-Amerikaanse oorsprong, die bij ons zelden gekweekt wordt. Volgens BOOM, Flora der gekweekte kruidachtige gewassen, 1950, p. 227 komt zij in collecties wel eens voor, terwijl een witte vorm ervan zeer zelden in tuinen wordt gekweekt. Of de vondst bij Arnhem als een verwilderde sierplant te beschouwen is, of dat de soort hier op andere wijze werd ingevoerd, is onbekend. Het geslacht *Chelone* L. is nauw verwant met *Penstemon* Mitchell, waarvan ook een aantal soorten als sierplanten bekend zijn en verschilt ervan door de aarvormige, onvertakte bloeiwijze, de in de oksels van brede schutbladen geplaatste, bijna zittende bloemen, de helmdraad van de steriele meeldraad, die korter is dan de andere helmdraden, de dicht wollig behaarde helmknoppen en de afgeplatte, gevleugelde zaden. Bij *Penstemon* is de bloeiwijze een pluim of tros of bestaat uit gesteelde bijschermen, de bloemen zijn gesteeld en de schutbladen smal; de steriele en fertiele meeldraden zijn ongeveer van gelijke lengte, de helmknoppen zijn kaal of stijfharig, de zaden niet afgeplat en ongevleugeld.

GRAY's Manual of Botany, 8th ed., 1950, herzien door FERNALD, waaraan ik deze gegevens ontleen, beschrijft de soort als volgt: "Stem 0,4—2 m high; leaves narrowly to broadly lanceolate or narrowly ovate, with short winged petiole or subsessile, acuminate, serrate; spike subtended at base by well-developed leaves, at first dense, elongating and loosening in fruit; bracts acuminate; sepals rounded, scarious-margined, obscurely or not at all ciliolate; corolla 2,3—3,5 cm long, creamy-white below, the summit and lobes roseate, purple or greenish-yellow, the lower lip with white to pale yellowish beard; the sterile filament greenish, much shorter than fertile ones; capsule globose-ovoid, 1—1,5 cm long."

Aan het slot van de beschrijving vermeldt FERNALD, dat de soort zeer variabel is. Hij onderscheidt behalve de typische *C. glabra* een drietal variëteiten, benevens enige vormen. Het bij Arnhem gevonden exemplaar moet tot de typische *C. glabra* gerekend worden. Voor deze geeft FERNALD als standplaats op: "low grounds, margins of streams, swales and wet thickets". *C. glabra* komt voor in Oostelijk Noord-Amerika van Newfoundland, Ontario en Minnesota in het Noorden tot Missouri, Alabama en Georgia in het Zuiden.

20. **Veronica beccabunga** L. var. **rubra** nov. var. floribus phoeniceis nec roseis. Op de Unio Swalmen werd aan de Maasoever bij Asselt in S 6.44.41 bij een grindgraverij een *V. beccabunga* met intens steenrode bloemen gevonden. Prachtig diep rood van kleur, even intens als het blauw van de gewone vorm. Omtrent roodbloemige vormen van *V. beccabunga* vind ik in ROUY Fl. de Fr. XI (1909) p. 39: "var *limosa* Math. Fl. Belgique 1, p. 397; *V. limosa* Lej. Fl. Spa p. 2; *V. Beccab.* var. *bracteata* Bréb. Fl. Norm. ed. 3 p. 215. — Feuilles subentières; bractées plus longues que les pédicelles; corolle ordt. d'un beau rose." De beschrijving door LEJEUNE van *V. limosa* luidt in Rev. Fl. Spa (1824) p. 2 "Foliis ellipticis, obtusis, breviter petiolatis, serrulatis; calycibus quadripartitis; bracteis lanceolatis pedicello longioribus; caule procumbente, radicante; floribus pallide rubris. Obs. Cette plante ne diffère du no. 15 (d.i. *V. Beccabunga*) que par la longueur de ses bractées et la couleur d'un rouge tendre des fleurs. Elle habite les bourbiers près Battice, Charneux etc. et se reproduit par le semis."

Ook G. Schlenker noemt in zijn artikel: Systematische Untersuchungen über die Sektion *Beccabunga* der Gattung *Veronica* in Beih. Fedde Rep. spec. nov. 90 (1936) p. 33 de "var. *limosa* (Lej.) Math., Fl. Gen. Belg. (1853) p. 397: Blüten blassrot, Deckblätter länger als die Fruchtstiele."

Im Herbar Berlin befindet sich ein hierhergehöriges, als *V. Beccabunga v. limosa* Lej. bestimmtes Exemplar: De Wever, Maastricht, 15 VII. 1906 mit der Notiz: "Blumen rosa, samenfest." Die Deckblätter sind hier etwa so lang oder etwas länger als der Fruchtstiel. Bei den blaublühenden Formen der Art sind die Deckblätter meist kürzer, selten so lang oder länger als die Fruchtstiel."

Ik heb zelf in mijn herbarium een exemplaar, waarbij in het handschrift van De Wever staat "*Veronica beccabunga* var. *limosa* Lej. Heugem (Koebroek)", waarbij ikzelf geschreven heb: "bloemen rood! leg. A. de Wever 1916." Nu is het Heugemmerbroek vlak bij Maastricht en voor iemand, die het handschrift van De Wever kent, is het niet vreemd, dat het mij waarschijnlijk lijkt, dat het jaartal 1906 bij het exemplaar in Berlijn en 1916 in mijn herbarium op dezelfde vondst betrekking heeft.

Intussen wordt in al deze citaten omtrent de bloemkleur gesproken van "pallide rubris", "rouge tendre", "blassrot", "rosa", wat voor de plant van Asselt absoluut niet kan gelden, vandaar dat ik deze als een nieuwe var. beschreven heb.

21. **Satureja vulgaris** (L.) Fritsch f. **albiflora** Sonck, in Memor. Soc. pro Fauna et Flora Fennica 13 (1937) p. 109 = *Clinopodium vulgare* L. fl. *albis*. Hoewel Oudemans in zijn Flora van Nederland 2 (1861) p. 360 omtrent de bloemkleur zegt: "De bloemkronen .... hebben doorgaans eene roode, soms echter ook eene witte kleur", Heukels in zijn verschillende flora's: "purper, zelden wit" en Hegi in Ill. Fl. Mitt. Eur. V. 4 (1927) p. 2296: "Krone karminrot, an einzelnen Individuen nicht selten weiss" wordt in de Prodr. Fl. Bat. Vol. I. Pars III (1904) p. 1286 van geen enkel witbloemig exemplaar melding gemaakt en had ik er zelf noch in herbaria noch in het veld ooit een ontmoet, tot ik een exemplaar in handen kreeg verzameld door K. Hana 17 Augustus 1950 in de duinen van de Amsterdamse waterleiding.

22. **Salvia reflexa** Hornem. Enum. Pl. Hort. Hafn. 1 (1807) p. 34. In A revision of *Salvia*, subgenus *Calosphace* by Carl Epling (Fedde Rep. Beih. CX 1939) behoort de soort tot de Sect. *Glareosae*, waartoe men in de Clavis sectionum l.c. p. 5 komt door de eigenschappen: *A A.* Stamina sub labiam superiorem ascendentia et in galea omnino inclusa. *B B.* Calycum labia superior 5—9-venis et ultra. *C.* Flores in glomerulis bracteis perstatis. *D D.* Staminum gubernacula vel integra vel ad connexum in dentem retrorsum interdum extensum dilata. *E E.* Pili simplices. *F F.* Herbae sat amplae vel frutices rarius tenellae. *G G.* Corollarum caerulearum rarius albarum tubi 2,5—9 mm longi. *H.* Styli imprimis glabri rarius sparse hispiduli. *I.* Styli ramus posticus quam anticus patentim brevior. *J.* Plantae continentis erectae annuae

foliis plerumque elliptico-oblongis" en waarvan de beschrijving luidt l.c. p. 102:

"Herbae annuae erectae ramis saepius cymoso-dichotomis hirtellis rarius pilis extensis longioribus sparse vestitis; foliorum laminis maximam partem elliptico-oblongis et in basi angustatis; floribus 1—3 in verticillastris bracteis nunc perstatis nunc deciduis subtentis, glomerulis in spicis interruptis dispositis; calycum labiis superioribus 5-venis; corollarum tubi subcylindratis intus nudis, interdum papillis minutis intus ornatis, labia superiore interdum subfalcata; staminum in galea inclusorum jugis ad medium connexis, gubernaculo oblongo in dentem retrorsum vel extensum dilato; stylis glabris vel ad apices sparse hispidulis, ramo antico obtuso in duobus speciebus quam superior longiore et plano-dilato; gynobasis cornu ovula subaequante. Species typica est S. hirsuta. Herbae in America septentrionali late disseminatae sunt." Tot de soort komt men dan l.c. door de eigenschappen:

"Bracteae perstatae vel tarde deciduae; folia 3 ad 20 mm lata.
  Bracteae maximam partem 2—6 mm longae.
    Styli ramus anticus obtusus; corollarum labia superior 2,5—3 mm alta." Daarna volgt dan de beschrijving van de soort:

"**S. reflexa** Hornem. Enum. Pl. Hort. Hafn. 1, 34, 1807 — *S. lanceolata* Brouss., App. Elench. Pl. Hort. Monsp. 15, 1805 (non Lamarck Illustr. 1, 72, 1791) — *S. lanceaefolia* Poir., Encycl. Suppl. 5, 49, 1817. — *S. aspidophylla* Roem. et Schult. Syst. Mant. 1, 206, 1822. — *S. trichostemoides* Pursh. Fl. Am. Sept. 1, 19, 1814.
Herba annua erecta ramosa, altitudine ad 60 cm ramis dichotomis ascendentibus retrorse hirtellis, internodiis 3—8 cm longis; foliorum laminis 3—5 cm longis, 3—12 mm latis, oblongis, etiam linearibus, obtusis, in basi ad petiolos hirtellos 0,5—1,5 cm longos angustatis, margine remote serrata, subintegra, pagina superiore glabra inferiore maximam partem pilis crispulis cinereo-hirtella; floribus saepius solitariis rarius 2—3 in verticillastris bracteis 2—3 mm longis lanceolatis hirtellis tarde deciduis subtentis, glomerulis inter se 1—2 cm distantibus; calycibus florentibus 4—6,5 mm longis, extus ad venas hirtellis, in maturitate plerumque 7—8 mm longis interdum 6 mm, rarius 9 mm longis hiantibus, pedicellis 2—3 mm longis elatis; corollarum tubo 4—4,5 mm longo, intus nudo vel frequenter papillis minutis binis ornato, labia superiore 2,5—3 mm alta, erecta, inferiore subrotunda, 4,5—5 mm diametro; styli ramo postico attenuato quam anticus obtusus multo longiore."

Blijkens de dan volgende lijst van vindplaatsen komt de soort voor van Illinois tot Mexico. In ons land werd de soort ontdekt door W. J. Reuvecamp Jr begin October 1948 te Deventer op het aloude Pothoofd, dat toen, voor het eerst na de oorlog, weer een zekere opbloei vertoonde. Het lukte ons toen met de determinatie niet verder te komen dan *Salvia*. In het voorjaar van 1949 nam ik de plant, met een aantal andere indeterminaten, mee naar Kew en liet ze daar aan verschillende Engelse adventieven-kenners zien, maar ook dat bracht mij niet veel verder; we hadden er trouwens ook niet veel tijd aan kunnen besteden. Toen echter Mr N. Y. SANDWITH in Augustus 1949 te Dagenham in S. Essex een *Salvia* vond, die hij als *S. reflexa* determineerde [zie zijn publicatie in Watsonia Vol. 1 Part. V (1950) p. 317] herinnerde hij zich mijn plant en was zo vriendelijk mij op een en ander attent te maken. Naar aanleiding daarvan hebben wij in Leiden de plant van REUVECAMP nog eens gerevideerd en als *S. reflexa* herkend. Omtrent de verspreiding van de soort zegt GAMS in HEGI Ill. Fl. Mitt. Eu. V. 4 (1927) p. 2478: "Von Nebraska bis Arizona, Texas, Florida und Mexiko. In Europa öfters mit amerikanischen Grassamen (z.B. *Festuca pratensis*) und Getreide eingeschleppt so bei Bremen (1894), Basel (1914), Innsbruck (1902)." SANDWITH noemt l.c. p. 318 behalve Dagenham nog de beide Britse vondsten: "Fritton, Norfolk, in B.E.C. 1928 Rep., p. 634 (1929)" en "Sibbertoft, Northants, in B.E.C. 1938 Rep., p. 53 (1939)". In Herb. Lugd. Bat. No. 940, 81—103 ligt een plant uit het Queensland Herbarium, Botanic Garden Brisbane: *Salvia lanceolata* Brouss. Pittsworth, Southern Queensland. C. F. White, 6654, 27. 2. 1930. Very common weed, flowers light blue. Regarded locally as very poisonous to stock.

23. **Plantago lanceolata** L. var. **altissima** (L.) Koch = *P. altissima* L. Sp. II (1762) = *P. lanceolata* L. s. sp. *altissima* Rouy. Op 4 October 1950 verzamelde Dr BRAND bij Doesburg (N. 6. **56**. 43) een *Plantago lanceolata* van zeer grote afmeting. De bladen waren van 25 tot meer dan 50 cm lang, resp. 6—4½ cm breed en 7—5-nervig; de stengels 50—70 cm lang, veelribbig. Mijn materiaal er nog eens bij vergelijkend vond ik een exemplaar leg. KLOOS Rotterdam Juli 1919, dat door THELLUNG gedetermineerd was als var. vel subsp. *altissima* (L.) Rouy. Hegi Ill. Fl. Mitt. Eur. VI. 1. (1918) p. 185 noemt de plant *P. altissima* L. en geeft de beschrijving:

"Pflanze ausdauernd, 30 bis 100 cm hoch. Wurzelstock walzlich, kriechend, ein- bis wenigköpfig. Laubblätter alle in grundständiger Rosette, verlängert-lanzettlich, bis 30 cm lang, 2 bis 4 cm breit, 3- bis 7-nervig, in den kurzen Stiel allmählich verschmälert, entfernt gezähnelt, spärlich behaart, kahl werdend, am Rande mitunter gewimpert. Schäfte vielfurchig mit angedrückten Zweizackhaaren besetzt. Blütenähre kurz walzlich oder eiförmig, vor dem Aufblühen spitz, 2 bis 3 cm lang. Tragblätter dreieckig-eiförmig, spitz, breit-trockenhäutig berandet, hellbraun, an der Basis oft kraushaarig, länger als der Kelch. Kelch 3-spaltig, die beiden vorderen Kelchblätter zu einem 2-kieligen Blättchen verwachsen, die beiden hinteren frei, alle sehr breithautig berandet, mit braunem, zottig-wimperigem Kiel, am Rande gewimpert. Blumenkrone 3 mm lang, weisslich oder bräunlich mit kahler Röhre. Staubfäden 2 bis 3 mal so lang als die Blumenkrone, weisslich mit gelblich-weissen Antheren. Kapsel eiförmig, 4 bis 5 mm lang. VI bis VIII. Auf nassen Wiesen, in Auen. In Deutschland bisher nur in Westpreussen bei Thorn, in Oesterreich zerstreut, in der Schweiz ursprünglich fehlend."

Vergelijkt men deze beschrijving met die van *P. lanceolata*, dan ziet men, dat de verschillen eigenlijk alleen maar dimensionaal zijn. Ik voel er dan ook weinig voor om deze vorm als een afzonderlijke soort te beschouwen of zelfs als ssp. Wellicht is zelfs de benaming als var. nauwelijks gerechtvaardigd en zou forma voldoende zijn. Op mijn verzoek heeft Dr Brand de plant in kultuur genomen en ik heb zelf ook een exemplaar, dat hij mij toezond, in mijn tuin gezet om te zien, hoe zij zich het volgend jaar zal gedragen. Nadat ik het materiaal van Dr Brand ontving, is het mij opgevallen, dat ook in de omgeving van Dordrecht en o.a. bij Alkmaar in het najaar van 1950 *P. lanceolata* van zeer grote afmetingen voorkwam, mogelijk als gevolg van de koele zomer en het zeer natte najaar, zodat we dan dus met een klimatologische vorm te maken zouden hebben. Misschien geeft de kultuurproef hieromtrent uitsluitsel.

24. **Campanula portenschlagiana** Roem. et Schult. var. **major** hort. (door S. J. van Ooststroom).

Campanula portenschlagiana Roem. et Schult. is een soort, die afkomstig is uit het Noord-Westelijk deel van het Balkan-schiereiland (het oude Kroatië, Dalmatië en Bosnië-Hercegowina). Zij wordt bij ons als sierplant in tuinen gekweekt, evenals de grootbloemige var. *major* hort. Van deze var. werden exemplaren aangetroffen bij Willemsoord (Ov.), tussen kreupelhout, in Juli 1946 door de Heer A. Eisses te Woerden. Desgevraagd deelde de vinder nog mede, dat de planten voorkwamen in gezelschap van lage *Calluna vulgaris*, *Erica tetralix*, *Hieracium laevigatum*, *Genista anglica*, *Sarothamnus* en laag eikenhakhout. Er waren geen tuinen of huizen in de buurt. Habitueel vertoont de soort overeenkomst met de eveneens als sierplant gekweekte *C. garganica* Ten. van welke zij echter o.a. duidelijk verschilt door de vorm van de bloemkroon. Hayek in zijn Prodromus Florae Peninsulae Balcanicae 2 (1931) p. 533 en 534 zet *C. garganica* bij de soorten met "corolla rotata profunde 5-fida" en *C. portenschlagiana* bij die met "corolla infundibuliformis (vel rotata), non ultra dimidium 5-fida". Van de laatste soort geeft hij (l.c. p. 534) de volgende beschrijving: "Caules numerosi laxi, ascendentes vel prostrati vel penduli, breviter pubescentes. Folia breviter pubescentia vel subglabra, cordato-orbicularia, petiolata, crenato-serrata. Flores longiuscule pedicellati racemum vel paniculam laxam formantes. Calycis laciniae lanceolatae, corolla glabra infundibuliformi-campanulata ca. 2 cm longa coeruleo-lilacina multo breviores. In rupibus subalpinis."

Vergelijken wij deze beschrijving met de planten, die de Heer Eisses mij toezond, dan klopt deze geheel, op de beharing en de grootte van de bloemkroon na. De hier gevonden exemplaren zijn namelijk vrijwel kaal en zeker niet kort en zacht behaard, zoals Hayek schrijft. Roemer en Schultes in hun oorspronkelijke beschrijving, in Systema Vegetabilium 5, 1819, p. 93, zeggen echter o.a. "caulis glaber, ut tota planta". De tegenstrijdigheid hierin wordt waarschijnlijk opgelost door een opmerking van Witasek op het etiket van het exemplaar van *C. portenschlagiana*, dat werd uitgegeven in de exsiccaten-collectie Flora exsiccata austro-hungarica, no. 3309 (Dalmatia. In rimis umbrosis rupium montis Biokovo, leg. Pichler). Witasek schrijft daar: "Die Beschreibung von *C. Portenschlagiana* in Roemer et Schultes Systema bezieht sich auf eine kahle Form. Auch bei dieser Art kommen aber, geradeso wie bei *C. pusilla* Hänke, behaarte und kahle Formen neben einander vor, so dass man dieselben nur als Varietäten einer Art betrachten kann. Es dürfte wohl in der Gattung *Campanula* der Grad der Behaarung überhaupt nich von systematischem Werth sein". Hieruit blijkt, dat het type van Roemer en Schultes zo'n kale vorm dezer soort is.

Wat de lengte van de bloemkroon betreft geeft Hayek ca. 2 cm op, terwijl Roemer en Schultes schrijven "corolla cum germine 3/4 circiter pollicis". Met inbegrip van het onderstandige vruchtbeginsel bedraagt de lengte van de bloemkroon hier dus bijna 2 cm. Het hierboven genoemde exemplaar 3309 van de Flora exsiccata austro-hungarica heeft bloemkronen van 1,5—1,8 cm lengte. Deze maten komen ook voor bij hier te lande gekweekte exemplaren van de soort. De planten van Willemsoord hebben bloemkronen van bijna of volledig 2,5 cm lengte en kunnen dientengevolge worden gerekend tot de var. *major* hort. Afbeeldingen van var. *major* zijn te vinden in The Garden 63, Febr. 1903, p. 110 en in The Gardeners' Chronicle 3. ser., 48, July 1910, p. 58.

25. **Cucumis melo** L. var. **agrestis** Naud. f. **africanus**. De monografie van Cogniaux en Harms in Englers Pflanzenreich (1924) voert in de tabel op blz. 117 tot de soort door de eigenschappen:

"A. Fructus laevis, glaber vel pubescens.
  a. Ovarium dense molliterque villosum vel setulosum.
    α. Foliorum lamina basi cordata, non sagittata.
      I. Lamina non latior quam longa.
        1. Lamina ambitu suborbiculari-reniformis.
          Annuus; lamina 5-angulata vel leviter lobata, molliter villosa vel scabriuscula; flores breviter pedunculati, masculi fasciculati. — Afr. trop., As. austral., in reg. calidior. cult."

De beschrijving luidt l.c. p. 120:

"*C. melo* L. Spec. ed. 1 (1753) 1011. — Annuus. Caulis repens, ramosus, hirsutus, elongatus, angulatus, demum quasi teres et glaber. Foliorum petiolus gracilis vel robustiusculus, hispidus, lamina aequalis vel longior; lamina suborbicularis vel ± reniformis, basi cordata, utrinque molliter villosa vel subhirsuta, 8—15 cm longa lataque, 5-angulata vel modice 3—7-lobata, lobis plerumque parvis, rotundatis, obtusis, denticulatis. Flores masculi fasciculati; pedunculi graciles, 0,5—2 cm longi. Receptaculum anguste campanulatum vel subcylindricum, longe villosum, 6—8 mm longum. Sepala subulata, erecta vel patula, receptaculo breviora. Corolla 2 cm longa, segmentis ovato-oblongis, acutis. Staminum filamenta glabra, brevissima; antherae 3—4 mm longae; appendix connectivi anthera duplo vel triplo brevior. Pistillodium 1 mm longum. Pedunculus femineus robustus, 1—2 cm longus. Stylus 1—2 mm longus, stigmate conniventia, 2 mm longa. Fructus polymorphus, pubescens vel glabratus. Semina sordide alba, oblonga, immarginata, basi subacuta, apice obtusa, 10—12 mm longa, 5—7 mm lata."

De var. *agrestis* wordt dan l.c. p. 121 beschreven: "Planta gracilis. Flores parvi, breviter pedunculati, saepius geminati vel terni. Fructus oblongus vel turbinatus, vix crassitudine pruni communis, non edulis."

In de "Zusatz über Melonen-Sorten (von H. HARMS)" l.c. p. 123 wordt de enorme variabiliteit van *C. melo* besproken en in extract de indeling van CH. NAUDIN [in Ann. sc. nat. 4 sér. XI (1859) p. 34] in 10 hoofdgroepen gegeven. Van de 10. Reihe *C. melo agrestis* Naud. heet het dan l.c. p. 126: "Hierhin gehören alle jene kleine Varietäten, die jetzt im wilden Zustande gefunden werden, entweder in den Heimatsgebieten der Art oder in solchen, wo die Art, wenn nicht heimisch, sich doch einbürgern konnte. Offenbar lieferte die Art bereits am Beginn ihrer Kultur dem Menschen gut unterschiedene Varietäten, und unsere gegenwärtigen kultivierten Sortenreihen gehen wahrscheinlich zurück auf ebensoviel verschiedene Varietäten, die sich einander parallel durch jahrhundertelange Kultur verändert haben. Es gibt zunächst 2 Gruppen wilder oder in den Wildzustand zurückgekehrter Varietäten. 1. Indische Wildmelonen etc. 2. Kleine Figari-Melone, wilde Afrika-Melone (Petit Melon de Figari, Melon sauvage d'Afrique). Fr. im typischen Falle obovoid, etwas nach dem Stiele verschmälert, meist zahlreich, von Hühnereigrösse oder kleiner, anfangs schwarzgrün, mit helleren Flecken, später bleichgelb, von angenehmem Duft; Fleisch weisz oder gelblich, fade, mit unangenehmem Nachgeschmack; Samen (wie bei Chate und einigen anderen Sorten) von klebriger durchsichtiger zäher Pulpa umhüllt. Triebe schlanker als die der gewöhnlichen Sorten, sehr rauhhaarig, Blätter nierenförmig oder undeutlich gelappt, dunkelgrün. Heimisch in Oberägypten, in Nubien und Abyssinien; vielleicht weiter verbreitet. Dieser Form scheinen verschiedene Melonen-Sorten von Ägypten, Syrien und Nordafrika nahezustehen."

Op 10 Augustus en 8 September 1950 verzamelde ik bij de Tilburgse Wolwasserij, tezamen met verschillende andere adventieven van vermoedelijk Afrikaanse herkomst, prachtig materiaal van deze wilde Meloen, met vrijwel rijpe vruchten. Deze waren van de bovenomschreven vorm, ongeveer 5 cm lang en 2,4 cm breed, lichtgroen, getekend met donkerder groene vlekken.

26. **Scabiosa columbaria** L. f. **prolifera** f. nov. Capitula secundaria parva e capitulis primariis deducta.

Deze vorm werd mij toegezonden door BR. MAURENTIUS, die haar op 3 Augustus 1950 bij Wahlwiller verzameld had. Het schijnt een analoge vorm te zijn met *Bellis perennis* L. f. *prolifera* hort., die in Engeland Hen-and-chicken-daisy genoemd wordt en die ik mij niet herinnerde ooit gezien te hebben. Toen ik de plant op de floristenbijeenkomst op 29 December vertoonde, bleken meerderen, o.a. JANSEN en HEIMANS, beter geheugen te hebben en een paar dagen later schreef VAN OOSTSTROOM mij: "*Scabiosa columbaria,* hen and chickens is hier (d.i. in het Rijksherbarium) aanwezig van de Riesenberg bij Gronsveld, leg. HENRARD, JANSEN, KLOOS en WACHTER 10—14 Juni 1916. Verder van Beek (L.), leg. J. M. VAN DEN HOUTEN, 10 Augustus 1939. Dit laatste lijkt zeer veel op jouw ex. Exemplaren van de Bemelerberg, waarop HEIMANS doelde, zijn ook aanwezig, doch vertonen geen "hen and chickens"; wel echter de opvallend kleine hoofdjes aan de zijtakken." Het eerste door hem genoemde exemplaar heb ik n.b. zelf in Ned. Kruidk. Arch. 1916, p. 77 genoemd met de woorden: "Ook verzamelden wij te Gronsveld een exemplaar, waarbij uit het hoofdje meerdere gesteelde hoofdjes van tweede orde komen".

27. **Senecio pseudovernalis** Zabel f. **pervernalis** C. T. Timme. Eind Mei 1950 schreef de Heer A. DE VISSER te St. Laurens op Walcheren mij over *Senecio vernalis* W. et K., die in zijn omgeving in 1948 en 1949 voorkwam en nu weer opgeslagen was en, vermoedelijk met *S. vulgaris* L., scheen te bastaarderen. Toen hij mij 6 Juni rijk materiaal van twee verschillende vindplaatsen toezond, bleek daar inderdaad de bastaard *S. pseudovernalis* bij te zijn en wel in de vorm *pervernalis*, die het meest bij *vernalis* aansluit en nieuw voor ons land is, daar de bastaard, die ik in "Aanwinsten 1940", Ned. Kruidk. Arch. 51 (1941) p. 120 vermeldde van Wychen leg. JOH. JANSEN veel dichter bij *S. vulgaris* staat en de naam f. *pervulgaris* C. T. Timme et Junge draagt. De bastaarden zijn, behalve aan hun intermediaire habitus, te kennen aan hun steriliteit.

28. **Senecio erucifolius** L. var. **bipinnatifidus** Van Ooststr., nov. var. (door S. J. VAN OOSTSTROOM). Fig. 5.
Zoals bekend is, vertoont *Senecio erucifolius* L. een grote variabiliteit in de vorm der veerdelige stengelbladen, de wijze van insnijding van deze en vooral in de breedte van de bladslippen. Bij de var. *communis* Rouy (fig. 5, c en d) zijn de zijdelingse hiervan ongeveer langwerpig-lancetvormig; de eindlob is meestal sterk ontwikkeld. Naar de ene zijde sluiten hierbij aan planten met veelal bredere bladslippen en nog grotere eindlob [var. *lyratus* Lagr. (fig. 5, a en b) en *latilobus* Boiss.], naar de andere met smallere slippen en smalle, weinig of niet bredere eindlob. Tot deze laatste behoort var. *tenuifolius* (Jacq.) A. et G. (fig. 5, e), waarbij de bladslippen lijn-lancet- of lijnvormig zijn, gaafrandig of voorzien van weinige, grove tanden.
Een plant door Prof. Dr S. E. DE JONGH samen met TH. J. REICHGELT in de Millingerwaard bij Nijmegen gevonden op 26 Augustus 1950 (H.L.B. 950. 325—169) overtreft var. *tenuifolius* nog in fijnheid van de bladinsnijding. De bij var. *tenuifolius* soms aanwezig zijnde grove tanden aan de bladslippen zijn hier veel langer, lijnvormig en groter in aantal, zodat het blad dubbel veerdelig wordt; soms vertonen de uiterste slippen nog weer een of weinige tanden. Evenals bij var. *tenuifolius* zijn de randen der bladslippen omgeslagen; de omtrek van het blad is breder dan bij deze var., nl. niet langwerpig doch ovaal tot omgekeerd eirond, terwijl de bladen ook minder tegen de stengel

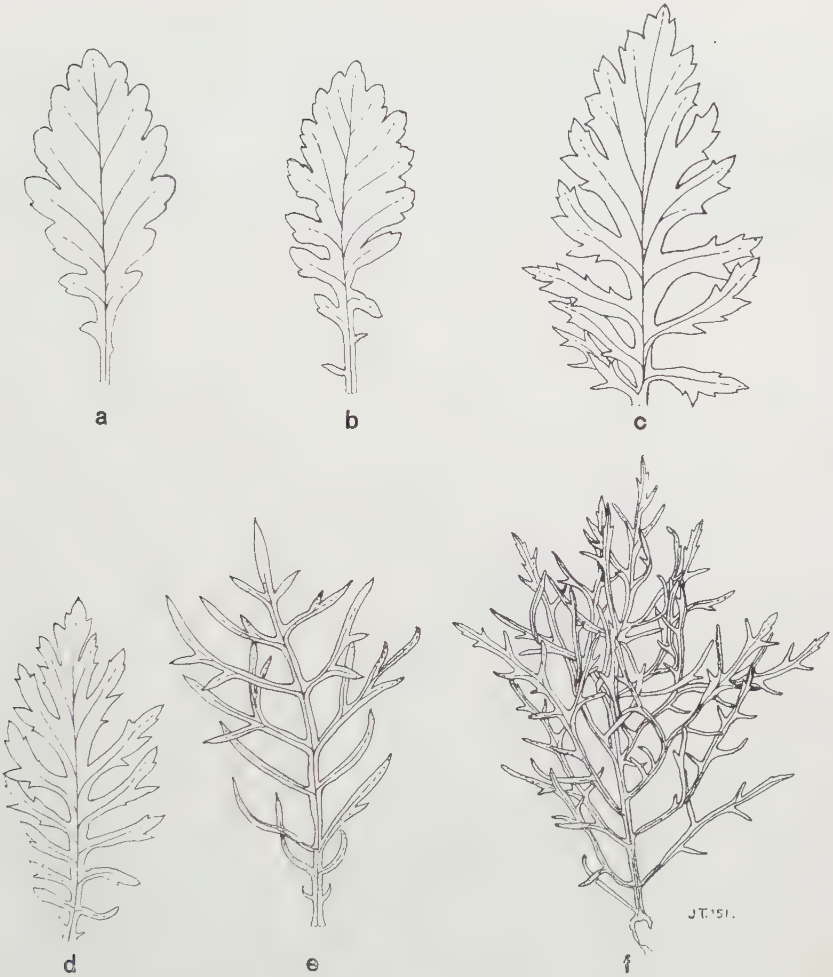

Fig. 5. *Senecio erucifolius* L., *a.*, *b.* var. *lyratus* Lagr.; *c.*, *d.* var. *communis* Rouy; *e.* var. *tenuifolius* (Jacq.) A. et G.; *f.* var. *bipinnatifidus* Van Ooststr.

zijn aangedrukt. De Latijnse beschrijving dezer nieuwe var. **bipinnatifidus** luidt: folia ambitu elliptica vel obovata, bipinnatifida, segmentis linearibus, margine revolutis (fig. 5, f.).

29. **Arctium minus** Bernh. ssp. **eu-minus** Bosw.Syme, met ± laciniate bladen (door S. J. VAN OOSTSTROOM). Fig. 6.
Een merkwaardige plant van *Arctium minus* Bernh. werd door Prof. Dr S. E. DE JONGH in Juli en Augustus 1950 waargenomen op een terrein bij het station te Leiden. Materiaal ervan bevindt zich in het Rijksherbarium sub no. 950. 240—748. In September daaraanvolgende had ik gelegenheid samen met Prof. DE JONGH nog meer materiaal van dezelfde plant te verzamelen, dat eveneens in het

Rijksherbarium werd gedeponeerd (no. 950. 261—370 en 375). De plant viel dadelijk op door de sterk afwijkende vorm der middelste en bovenste bladen. Deze waren nl. langwerpig tot smal-eirond, onregelmatig grof getand tot gelobd en liepen aan de basis smal wigvormig in de bladsteel uit, geheel op dezelfde manier als bij sommige laciniate vormen van andere plantensoorten het geval is. De onderste bladen waren breder en kwamen daardoor meer met de normale overeen, hoewel ook hun bladrand dezelfde grove tanding vertoonde en hun basis ook wigvormig in de steel versmald was.

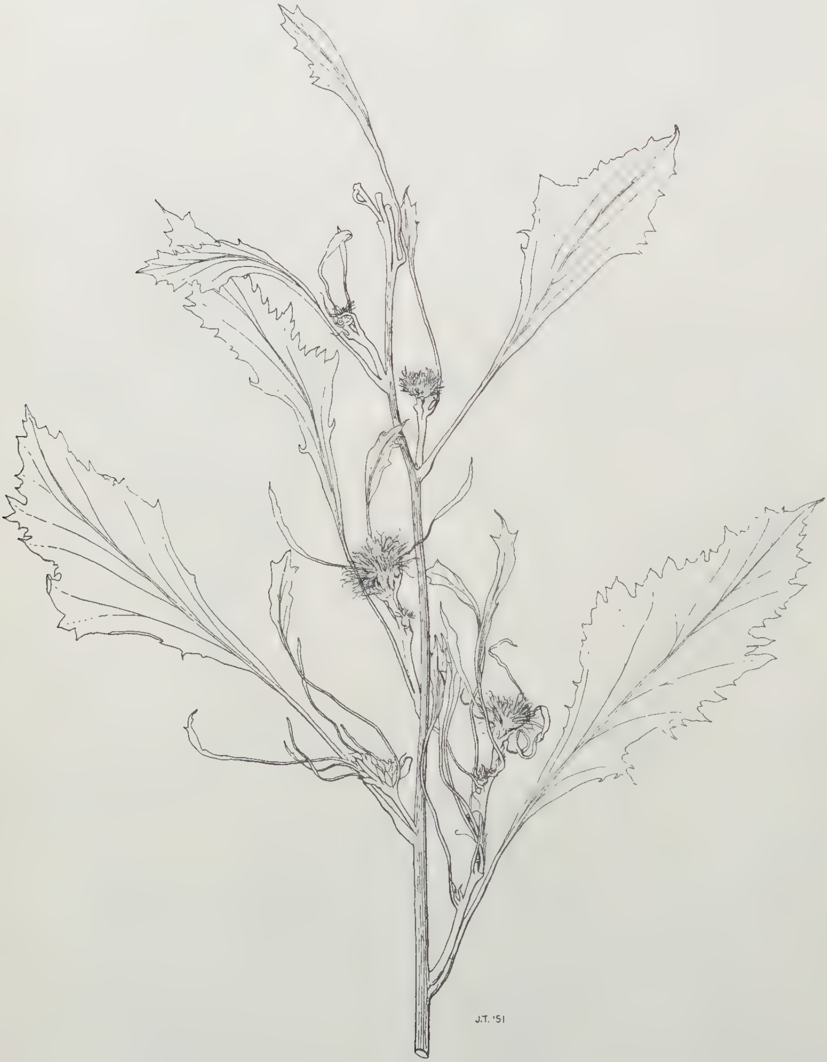

Fig. 6. *Arctium minus* Bernh. ssp. *eu-minus* Bosw. Syme, met ± laciniate bladen, deel van een zijtak.

J. Arènes, die in zijn onlangs verschenen monografie van het geslacht *Arctium* (in Bulletin Jard. Bot. de l'État, Bruxelles, 20, 1950, p. 67—156) diverse kleinere taxa beschrijft, maakt geen melding van een dergelijke laciniate vorm. Naar aanleiding van photo's van de plant, die ik deze monograaf toestuurde, deelde hij mij mede, dat zo'n vorm hem niet bekend was. Tegelijkertijd wees hij erop, dat zijns inziens deze vorm waarschijnlijk van weinig systematische waarde was en niet de moeite waard om beschreven te worden. Het eerste kan zeer zeker het geval zijn, maar toch komt het mij voor, dat het steeds van belang is om dergelijke en zeker zulke opvallende afwijkingen in de botanische literatuur vast te leggen, al was het alleen maar om er de aandacht op te vestigen. Hoe dikwijls heeft dit niet tot nieuw onderzoek of tot nieuwe vondsten geleid.

Tracht men na te gaan, bij welke der door Arènes in zijn boven aangehaalde bewerking vermelde ondersoorten onze plant behoort, dan valt de keuze op ssp. *eu-minus* Bosw. Syme. Het aanwezig zijn aan de hoofdstengel en de primaire takken van zijtakjes met meerdere zeer kort gesteelde of zittende hoofdjes wijst in die richting. Bij de andere eventueel in aanmerking komende ondersoort *pubens* (Bab.) J. Ar., zoals Arènes deze in zijn monografie aangeeft (vgl. hierbij ook de tekeningen op p. 93 van deze monografie) dragen deze zijtakjes over het algemeen slechts een enkel hoofdje. Bovendien vertoont de ssp. *eu-minus* aan genoemde zijtakjes steeds meerdere kleine bladen, wat bij ssp. *pubens* in mindere mate het geval is. Deze kleine bladen zijn ook bij de Leidse plant duidelijk te zien, hoewel zij veel smaller zijn dan bij typische exemplaren; zij zijn smal lancet- tot lijnvormig en aan de basis lang wigvormig in een lange steel versmald. De hoofdjes der plant zijn over het algemeen slecht ontwikkeld. Slechts enkele ervan bereiken de grootte van normale *A. minus*-hoofdjes. Terecht maakt Arènes dan ook de opmerking, dat de plant een monstrueuze indruk maakt, iets, wat bij laciniate vormen meer het geval is. Ook vertoont zij overeenkomst met planten, die door groeistoffen beschadigd zijn. Voorbeelden hiervan zijn te vinden in het door de Plantenziektenkundige Dienst te Wageningen uitgegeven vlugschrift no. 68, Dec. 1950, getiteld: Beschadigingen veroorzaakt door groeistoffen. Dat in ons geval een dergelijke beschadiging zou zijn opgetreden komt mij, wanneer men de standplaats der plant in aanmerking neemt, niet zeer waarschijnlijk voor; de plant werd nl. gevonden op een verwilderd terreintje in de onmiddellijke nabijheid van de werken voor het nieuwe Leidse station, een omgeving waar zeker niet met groeistoffen gewerkt is. Bovendien groeide zij samen met geheel normale planten.

30. **Crepis tectorum** L. f. **gracilis** Wallr. = *Crepis Lachenalii* Gochn., nec Gmel. Van deze vormenrijke soort, die nu eens sterk op *C. virens* lijkt en dan weer tot *C. biennis* nadert, vonden wij op de zomerexcursie van de Kon. Ned. Bot. Ver. te Swalmen, oostelijk van de plaats en ten zuiden van de Swalm in een korenakker een prachtige, homogene groep van planten, die door slanke habitus en alleen in de

bovenste helft vertakte stengel een zeer opvallende indruk maakten. Bij nader onderzoek bleken zij te behoren tot de f. *gracilis* Wallr., die in Hegi Ill. Fl. Mitt. Eur. VI, 2 (1929) p. 1166 als volgt beschreven wordt: "Alle Laubblätter lineal, ganzrandig, am Grunde nicht oder nur schwach pfeilförmig."

Volgens A. G. de Wilde, die binnenkort over het geslacht *Crepis* nader hoopt te publiceren, zou het aanbeveling verdienen de planten van Swalmen te rangschikken onder f. *segetalis* Roth = *Crepis stricta* Schulz, nec Scop. waarvan de beschrijving l.c. luidt: "Untere Stengelblätter breit lanzettlich, schwach gezähnt, die mittleren lanzettlich, fast ganzrandig, die oberen lineal, am Grunde schwach pfeilförmig. Stengel meist schlank und wenigköpfig."

IN VITRO STUDIES ON THE EMBRYO OF CAPSELLA BURSA-PASTORIS

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INTRODUCTION

The fertilized egg-cell or zygote must often be considered pre-eminently omnipotent. With many animals and also with lower plants the zygote develops independently in the external medium and all factors, needed for the growth and differentiation of the embryo, must be assumed to be present in the egg. The whole problem of morphogenesis is presumably comprised in the zygote itself, even though external factors may affect the development to a certain extent.

With higher plants as well as with viviparous animals things may be different. In Spermatophytes the zygote and later the embryo are embedded in the embryo-sack, the nucellus or the endosperm, and it seems likely that the surrounding tissue supplies the zygote and later the embryo with substances, needed for its development and differentiation. It may be presumed that this happens in a special pattern and according to a definite schedule. Even a very young embryo (globular stage) displays some differentiation in its basal-apical polarity. In later stages (heart-shaped stage) further important differentiation can be stated at the apical end: biradiate symmetry superseding the original polyradiate symmetry.

In this condition the fertilized egg-cell and the young embryo appear exceptionally suitable for the study of the differentiation and morphogenesis in dependency on the milieu by applying an in-vitro technique. The realization of such a technique probably would create a field of new possibilities for morphogenetic studies in various directions.

On the other hand, not only the problem of morphogenesis, but also that of the metabolism of the embryo has increased the interest of physiologists. Organisms that in later stages are completely autotrophic, start their life heterotrophically. Already a casual survey of the literature shows that the heterotrophism increases and that the medium has to comply with higher demands, the younger the embryos are. The knowledge of these demands is still very deficient. One of the reasons why very young embryos still cannot be cultivated is our lack of knowledge of the chemo-differentiation, protein-synthesis being one of the main problems of biochemistry.

A second reason why the cultivation of young embryos did not succeed satisfactorily, is that the physico-chemical conditions of the natural medium inside the ovule have not yet been studied, though this medium could yield valuable data, such as pH and osmotic value. As yet no one has deliberately tried to imitate the embryogenesis in the ovule. Several investigators mention a premature germination of the embryos in the culture; this abnormality is due to an insufficient knowledge of the factors controling this phenomenon.

Germination is defined here to start at the moment that the embryonic tissue — in a state of cell-division and plasmatic growth — becomes separated by an intercalated section of incipient cell-elongation. The appearance of cell-elongation marks off a new phase of the life-cycle, as it affects the nature of growth and structure essentially. So we emphasize the necessity of distinguishing between pregerminal and postgerminal cultures, both being quite different objects of investigation.

The purpose of our study was, to collect more information on the requirements for growing young embryos according to normal embryogenesis.

Our experiments have been conducted on *Capsella bursa-pastoris* (L) Med.. This choice was based on the following considerations: 1. The embryo of *Capsella* is the classic example of the dicotyledonous embryo, the development of which has often been described. 2. The plants are flowering for six months at a stretch and during this time yield all embryonic stages. 3. In the inflorescence these stages are arranged along the axis in silicles, the younger ones at the top, the older ones near the base, thus facilitating the search for specific stages. 4. Each silicle contains about 20—25 embryos of approximately equal lengths (so the application of statistical analysis would be possible). 5. Capsella embryos can easily be isolated.

We started by gathering some information about the embryo and its environment in the ovule. Chapter II contains these data.

Next we tried the culture of young embryos, making good use of the obtained information. A culture-method was developed that allowed daily examination and measuring of the growth, this being necessary for the analysis of several factors, especially of the nitrogen-source. These experiments have all been made on "torpedoes" and heart-shaped embryos, and will be recorded in Chapter III.

Finally, the viability of cultured embryos was tested in a post-germinal cultivation. The findings in this field are reported in Chapter IV.

The methods, used for the various purposes, will be described along with the experiments.

The disappointing fact that we did not yet succeed in cultivating globular embryos postponed our aspirations for the experimental-morphological range. However, this negative result may have its significance as will be shown in the discussion at the end of this paper.

Chapter I

SURVEY OF THE LITERATURE

In this survey we will confine ourselves to the discussion of those papers that deal with the cultivation of plant-embryos excised from the ovule during their embryogenesis.

Thus far in literature the name "embryo-culture" has mainly been used in the case of the cultivation of mature or even germinating embryos, which in order to make an analysis of their heterotrophy are deprived of their natural food-supply. In spite of the above-mentioned difference between pre- and post-germinal embryo cultures we cannot entirely omit the discussion of the latter as information gained by its study largely contributes to the successful pregerminal culture.

The first to realize the idea of cultivating immature plant-embryos *in vitro* was HANNIG (1904). He succeeded in making a sterile culture of embryos of Crucifers (mainly *Raphanus sativus*) when using TOLLENS' nutrient solution with 10 % sucrose as a medium for embryos of about 2 mm in length (8 mm when mature). The embryos were kept in this medium for 29 days and during that time they grew 1—2 mm. Then they were transferred to cotton-wool in a salt-solution and, having been planted out in earth after germination, they developed into flowering plants. Since he stated, that the growth-rate of the embryos in his medium decreased, he tried to improve the growth by changing the nitrogen-source; he tested peptone, aparagine, leucine, glycocoll and tyrosine. But this part of HANNIGS investigation, carried out on *Cochlearia*, cannot be considered sufficiently exact for a quantitative analysis. The number of cultures in one series was very small; the original lengths of the embryos were not the same and there was also a variation in the duration of the experiments. These results were all negative and are not conclusive. His finding of amino acids inhibiting the growth in concentrations of more than 0.1 % raises the surmise, that the medium had been altered unfavourably during the sterilization by heat. Moreover, his choice of amino-acids was rather inadequate, as will be learned from our results. HANNIG, however, could state the need of a high oxygen-tension in an experiment with two series of embryos; in one of the series the embryos were scarcely covered by the medium, while in the other series one or two cm sunken under its surface. He found an appreciable difference between the two series. Interesting from a morphological point of view is HANNIGS observation that the embryos do not bend when being cultivated, but remain straight.

A second paper on plant-embryo-culture did not appear until twenty years later: DIETERICH (1924). He worked on representatives of about fifteen plant-families, trying to find out whether embryos are able to germinate without having passed a resting-period. DIETERICH excised the embryos when nearly mature and cultivated them on KNOP solution with 1.5 % agar. Younger embryos could mostly be brought to germination also, when 2.5—5 % sucrose had been added. In the case of these younger embryos a difference in development could be stated between embryos, cultivated on top of the agar and others, cultivated under the agar-surface, the latter continuing the embryonic growth until mature length, whereas the former started germination precociously. This phenomenon, called "künstliche Frühgeburt" by DIETERICH, appeared later also in several other investigations, and gained special attention as a deviation of normal development.

The embryo-culture was used by LAIBACH (1925, 1929) as an expedient for growing hybrids of *Linum*-species that normally abort in the ovule. The embryos (1.5 mm) were excised and cultivated on cotton-wool in a solution with 15 % sucrose. This culture-period lasted for 18 days, at the end of which time the originally green embryos had become ivory in colour. Then they were transplanted on filterpaper and germination followed.

This may be considered a starting point for many later investigations. By means of the embryo-culture special hybrids were grown by: JÖRGENSEN (1928); WERCKMEISTER (1934); SKORSTEDT (1935); BENSLEY (1940); SKIRM (1942); LAMMERTS (1942); BLAKESLEE and SATINA (1944); SMITH (1944); BRINK, COOPER and AUSHERMAN (1944); CUMMINGS (1945); MAC LEAN (1946); SANDERS (1948, 1950); STONE and DUFFIELD (1950).

TUKEY (1933, 1934, 1938, 1944) brought in culture thousands of embryos of early-ripening species and varieties of stone-fruits that otherwise would have aborted in the seed.

An investigation of LAMMERTS (1942) is in the same line.

The embryo-culture served another purpose in the work of RANDOLPH (1945). He succeeded in shortening the life cycle of *Iris*-species by passing over the two years resting-period in the seed.

A further step in this direction was taken by COX, MUNGER and SMITH (1945), who excised embryos of *Brassica*, thus withdrawing them from the influence of inhibiting substances in the seed-coat.

The method of the embryo-culture has also been applied for the benefit of vernalisation-research, mainly by PURVIS. FOR a review of the literature in this field we refer to MURNEEK and WHYTE (1948).

TUKEY cultivated his embryos in small bottles on a nutrient-solution with 0.65 % agar and 0.5—2 % dextrose. Like DIETERICH he observed an aberrant embryo-development. This phenomenon roused his interest and in 1938 he published a study of it on peach-embryos. He found, that dwarfism in the seedlings was stronger the younger the embryos were when excised. Thus he distinguished a number of different "growth-patterns". After having been subdued to a thirty-days period of reduced illumination, all forms could grow into mature plants when brought back to the greenhouse.

Besides TUKEY several other investigators mentioned an abnormal morphogenesis of the cultivated embryos, and invariably the phenomenon turned out to be accompanied by precocious cell-elongation: LI (1934) on *Ginkgo*-embryos; LA RUE (1936) and LA RUE and AVERY (1938) on embryos of *Gramineae*. MERRY (1942) found "growth-patterns" for *Hordeum sativum*.

VAN OVERBEEK (1942 b) held the opinion, that a high "auxin"-concentration would keep the embryos in embryonic condition; he based this view a.o. on an observation by THIMANN (1937), who noted an inhibiting action of "auxin" on bud-development.

KENT and BRINK (1947) reported that tomato-juice and hydrolysate of casein prevented germination when added to a control-medium on which the embryos germinated readily. Continuing this investigation, ZIEBUR, BRINK, GRAF and STAHMANN in 1950 published the results of an analysis of this inhibition, that appeared to be due to inorganic substances in the casein-hydrolysate and they found that the same results could be obtained by using isotonic solutions of sucrose or mannitol.

In this connection it is worth noting that, whenever in the literature phenomena of the "künstliche Frühgeburt" are mentioned, investigators are sure to have been working with low sugar-concentrations, i.e. low osmotic values of the medium.

The view that the osmotic value of the medium is one of the factors determining the nature of the growth, is likewise supported by some findings of Duym, Komen, Ultee and v. d. Weide (1947) in this laboratory, viz. that the inhibition of germination by extract from *Beta*-seeds at least partly is due to the presence of osmotically active material.

Returning to the problem of the requirements of the medium we must state, that no notable progress was made in the pre-germinal embryo-culture until 1940.

Interesting and epoch-making in the field of plant-tissue-culture was a paper by White (1932); he was the first who added growth-factors to the medium though it was, conformably to the time, in the form of an undefined yeast-extract. On a medium consisting of a salt solution with only 2 % glucose and added yeast-extract he managed to grow, by way of random-test, a small (0.2 mm) heart-shaped embryo of *Portulaca oleracea* to a length of 1.84 mm in three weeks.

There is only one other publication of some importance to be mentioned, viz. that from Li and Shen (1934), who found a growth-promoting action on yeast-cells by extracts of rice and of wheat-bran; according to Williams these extracts contain pantothenic acid. On the growth of *Ginkgo*-embryos, however, they had an inhibiting effect, in this case growth-stimulation could only be obtained by adding low concentrations of an extract of *Ginkgo*-seed-endosperm.

During those years the post-germinal embryo-culture yielded more valuable results. In a series of investigations on mature or germinating decotylated *Pisum*-embryos, the favourable influence of several growth-factors was shown. Thus it became clear that Schopfers concept: "auxo-heterotrophy" could very well be applied to embryos (Rytz, 1939). Parts of this research were carried out by:

von Hausen (1935, 1936), who noted the influence of ascorbic acid on the growth.

Kögl and Haagen Smit (1936), who demonstrated aneurin (thiamin) and biotin as required growth-factors, whereas ascorbic acid did not promote growth;

J. Bonner and Axtman (1937), who stated a positive effect for pantothenic acid;

J. Bonner (1938), who did so for niacin;

J. and D. Bonner (1938), who once again mentioned ascorbic acid as an active growth-factor.

According to Rytz (1939) the discrepancy of these results is due to the fact, that different *Pisum*-varieties had been used. The probability of this view was endorsed by RYTZ himself by showing a difference in the activity of aneurin on different varieties. Moreover, SAUBERT–VON HAUSEN (1948) could actually confirm this opinion for ascorbic acid. She also tested other growth-factors, viz. vitamins B_1, B_2 and B_6, biotin and pantothenic acid, adding them to a salt-solution with 4 % sucrose, together with ascorbic acid. By simultaneous administration of these growth-substances an additional growth-response was obtained, but there still was a marked difference with control-seedlings with cotyledons.

It is only after 1940 that the experience, gathered from the experiments mentioned, has been employed in behalf of the pre-germinal embryo-culture.

Progress was made by an analysis of various growth-factors by VAN OVERBEEK, CONKLIN and BLAKESLEE (1942 a) on *Datura*. This was the first more extensive study on the culture of young embryos. Viable seedlings could not be obtained without adding growth factors to the medium that consisted of a nutrient solution with agar and 1 % glucose. Only when the cultivation was started with already bent embryos growth factors could be omitted, but younger embryos ("torpedo"-stage) needed growth substances such as glycine, aneurin, ascorbic acid, niacin, vitamin B_6, adenine, succinic acid and pantothenic acid, but the necessity of each of these factors apart was not demonstrated. Embryos smaller than 0.5 mm, however, did not thrive even on such a medium; addition of coconut-milk in this case gave rise to an enormous growth, e.g. from 0.15 mm to 6 mm in 7 days. Casually VAN OVERBEEK (1942 b) claims to have grown even pro-embryos (0.10 mm).

This strong growth-promoting effect of coconut-milk was accredited to an unknown "embryo-factor", supposed to be present in it. As a remarkable detail must be mentioned that the younger embryos started growing callus-like when the coconut-milk had been autoclaved. According to VAN OVERBEEK this abnormality might be due to an increase in the "auxin"-content, that could have resulted from the heating.[1] In the same paper he indicated also the presence of inhibiting substances in coconut-milk, e.g. a "root-inhibitor" that could be removed by shaking with alcohol.

Continuing the research on the optimal conditions for growing embryos, VAN OVERBEEK, SIU and HAAGEN SMIT (1944) not only tested several pH's and temperatures, but once more they investigated the composition of the medium. Sucrose was shown to be a far better source of carbon than glucose; as an explanation for this fact they suggest the difference in liability of the two substances to phosphorylation. Coconut-milk proved to be superior to natural extracts, such as those from yeast, from wheat-germs or from ovules of *Datura*, though these extracts did promote the growth in young embryos. Next the authors subjected coconut-milk to chemical purifications and finally acquired a product 170 times more active than the original sap. This preparation promoted the growth of *Datura*-embryos when added to the basal medium, containing 2 % sucrose, in a dilution of 1 : 19000, indicating hormone-activity of the "embryo-factor". The argument, however, is not conclusive, since a quantitative test, e.g. a concentration-series, is lacking.

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[1] In this connection we may refer the work by CURTIS (1947), who likewise achieved a noteworthy undifferentiated growth of *Vanda*-embryos, unto 1.5 ml, by adding barbiturates (10 p.p.m.) to the medium.

The coconut-milk was soon to lose its exclusive reputation as an exceptional growth-stimulant, for BLAKESLEE and SATINA (1944) demonstrated, again on *Datura*, that it could be replaced quite well by malt-extract, provided the latter had not been sterilized by heat, but by filtration. Heat-sterilization gave rise to inhibiting substances, but these could be dissolved in and removed with ether, as was shown by SOLOMON (1950).

For corn-embryos coconut-milk proved to be useless: HAAGEN SMIT, SIU and WILSON (1945) cultivated these embryos in order to find out the most adequate source of nitrogen. Asparagine worked very favourably and could bring down the limit of cultivability to 0.3 mm initial length, but addition of coconut-milk could not lower it further. This may be due to the low sugar-concentration.

SANDERS and BURKHOLDER (1948 a, b) were strongly interested in the problem of the nitrogen-supply. They first stated a notable growth and normal development of *Datura*-embryos when casein-hydrolysate had been added to the medium. The same results could be obtained when using a combination of all pure amino-acids instead, but this favourable effect could not be matched by incomplete mixtures or by single amino-acids. With respect to different species, viz. *D. stramonium* and *D. inoxia*, small differences in activity of the amino-acids were noted. Besides, the authors noticed some diversity of development of embryos, cultivated in various incomplete mixtures, the ratio between cotyledons and hypocotyl being affected. The conclusion from these results was as follows: "The growth-stimulus of the concentration of 20 acids results from the physiological interaction rather than from the summation of effects of individual acids".

Perhaps this conclusion also includes the explanation of the negative results of SPOERL (1948); he tested 19 single amino-acids as a source of nitrogen for Orchid-embryos, mostly seeds of *Cattleya*. At most some amino-acids equalled the effect of ammonium nitrate. The autoclaving of his media, however, raises some doubt as to the reliability of these results.

RAPPAPORT, SATINA and BLAKESLEE (1950) tried the influence of ribonucleic acid and desoxyribonucleic acid on *Datura*-embryos. The effect was rather an inhibition than a growth-promotion, even in a concentration of 0.0001 p.p.m..

Finally we must mention two publications, dealing with the differences in reaction between species of one genus or between hybrids. The investigations were carried out again on *Datura*-species.

DOERPINGHAUS (1947) cultivated ten different species on various

PLATE V

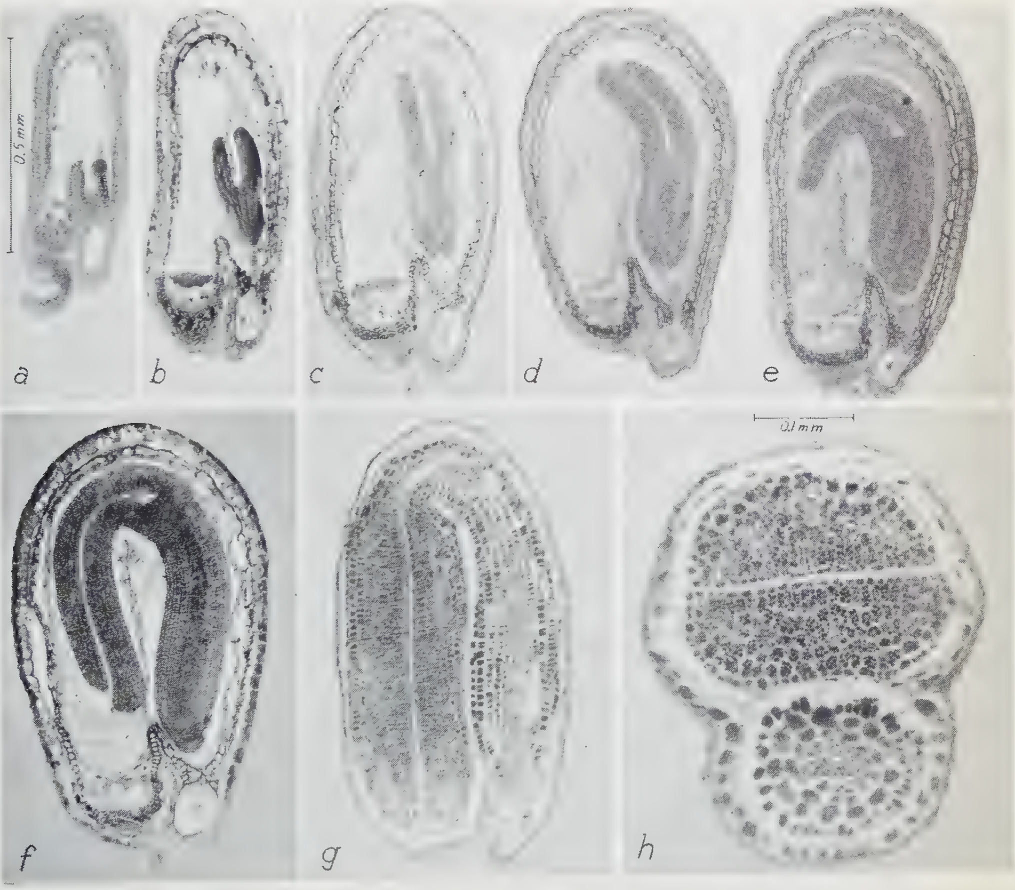


Fig. 1. Microphotographs of histological sections through ovules of different stages. a—f: developing ovules; g and h mature seeds. All reproductions at the same scale except h, which shows the transsection of the seed with abundant aleurone grains in the embryo. Fixation after Land; staining with gentianaviolet.

sugars. Though sucrose proved unalterably superior, other sources of carbon (mannose, dextrose, laevulose, glycerol, a.o.) did not act equally on the different species.

A similar fact could be stated by SANDERS (1950). The optimal sucrose-concentration appeared to be different for *D. stramonium* and three other species. Likewise those species did not show the same dependence on $(NaPO_3)_n$ (= "Calgon") concentration. In this paper also tests with growth substances are reported: various synthetical "auxins" (10 p.p.m.) did not stimulate the growth, nor did the growth substances mentioned by VAN OVERBEEK, CONKLIN and BLAKESLEE (1942). The growth-promoting action of malt extract would be due to soluble nitrogen containing substances, this extract being rich in amino-acids (DICKSON and BURKHART, 1942), that are known to promote growth.

CHAPTER II

THE EMBRYO IN OVULO

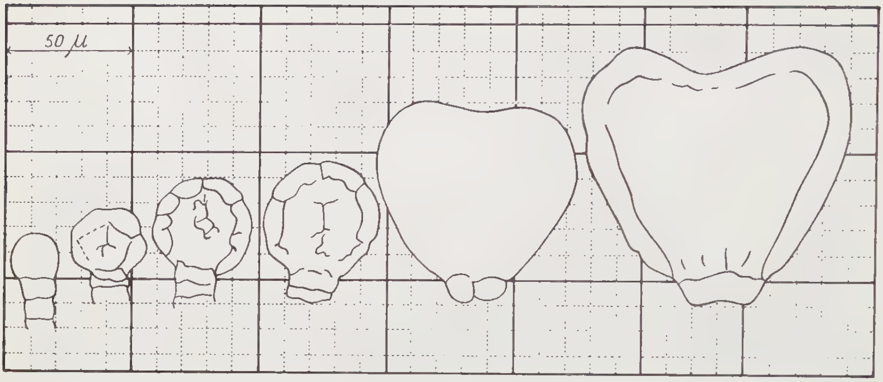
A. THE EMBRYO

§ 1. *Classification of the stages in embryogenesis*

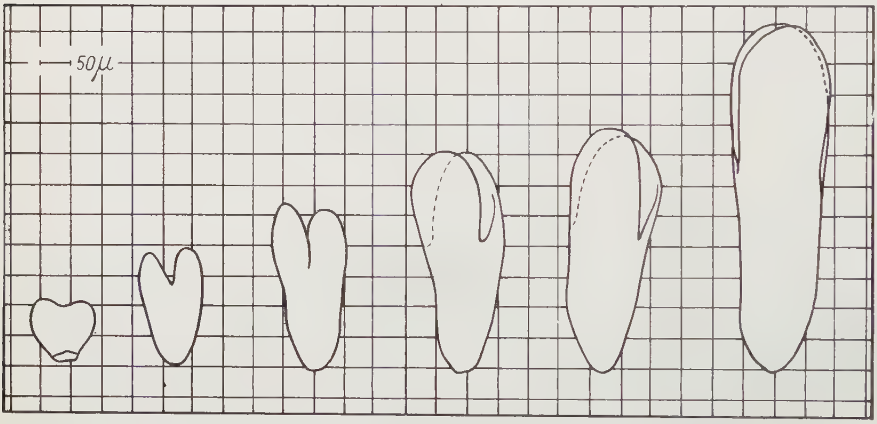
The embryogenesis of *Capsella bursa-pastoris* has been studied regularly, since HANSTEIN for the first time did so in 1870. As for the development up to the globular stage, the most exact description is that by SOUÈGES (1916,1919).

Our own observations led to a classification of the whole development, which is given in table I and figure 2. The position of the embryo in the campylotropic ovule at various stages may be seen from the micro-photographs of histological sections (figure 1). Even in the younger stages, the nucellus is failing; the endosperm is of the nuclear type; in the mature seed only a layer of aleuron-filled cells is left of it, like in other Crucifers (GUIGNARD, 1893). According to the terminology of A. P. DE CANDOLLE the situation of the embryo in the seed is notorrhiz.

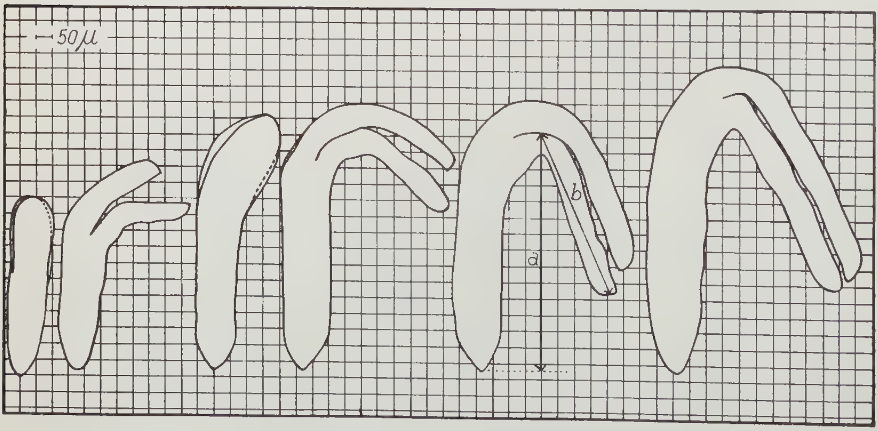
When freshly excised from the ovules, the embryos are green up from stage IV. As the embryo grows older, the colouring becomes stronger. Yet embryos from mature seeds are hard and ivory-white. No starch can be found in their cells then, while aleuron-grains and fats are abundant. In younger stages starch occurs, but not earlier than in stage IV. In this "intermediate" stage not more then a few cells contain very small grains, visible only when magnified 400 ×. Up from the torpedo-stage, starch grains are big and numerous enough to be noticed when magnified only 100 × ; most of them are located in the hypocotyl. It is certain, that fats are present in the embryos in stage V (torpedo) and in older stages; they quite probably are synthesized from the starch.



Stage I to IV



Stage III to VI



Stage V to VIII

Fig. 2. The stages of the development of the embryo.

TABLE I

The stages of development of the embryo *in ovulo*

Stage	Length*	Shape
I	18— 50 μ	globular.
II	50— 80 μ	reversed trapezium; height and breadth equal, third dimension somewhat smaller.
III	80— 150 μ	heart.
IV	150— 350 μ	intermediate between III and V, characterized by longitudinal growth of the cotyledons and of the hypocotyl to a slightly less extent.
V	350— 700 μ	"torpedo"; the cotyledons are flattened against each other and take half the length of the embryo.
VI	700— 900 μ	"walking-stick", caused by the cotyledons having turned back in the top of the ovule.
VII	900—1700 μ	upturned U, the one leg formed by the hypocotyl, the other by the flattened cotyledons.
VIII	1760 μ	full-grown embryo.

* without suspensor.

§ 2. *The variation in length of the embryos from one silicle*

As it was necessary to get an idea of the variability of the embryos, contained in one silicle, we gathered 10 silicles from 2 well-grown plants and measured the embryos. The mean number of ovules per silicle was 24.1 (with standard deviation 3.3).

As the different silicles contain embryos of different stages and sizes, the standard deviations of the embryo length per silicle in their absolute values would only yield incomparable data. In order to obtain a uniform measure each standard deviation was expressed in a percentage of the mean embryo length of the silicle in question. After this the 10 thus computed standard deviations were averaged. From these calculations a mean value (14.8 %) resulted with a small standard error (0.6 %). As appears from these data the variability is constant; this is mainly due to the presence in many silicles of an odd small embryo.

Comparison of the mean lengths of embryos, derived from the two separate halves of one and the same silicle, however, gave no greater difference than 3.8 % of the lower value.

§ 3. *The correlation between the lengths of silicles, ovules and embryos*

In order to avoid a laborious search for definite stages when starting a culture, we tried to estimate beforehand the relation between the lengths of silicles, ovules and embryos on racemes of several plants.

Though there is some difference between the plants, they all show the same characteristics that are presented in figure 3a; this graph gives the data from one well-grown plant. On the abscis, the numbering of the silicles is plotted, the numbers 1, 2, 3a etc. indicating the first, second, third etc. silicle from top to base, starting with the youngest silicle without petals. The numbering — 1, — 2, — 3 etc. therefore goes upward from the undermost silicle with petals. Thus the abscis may be understood as a time scale. On the left ordinate, the lengths of the silicles are set off, and on the right ordinate on a larger scale those of ovules and embryos. In figure 3b the embryo length is plotted directly against the size of the silicle.

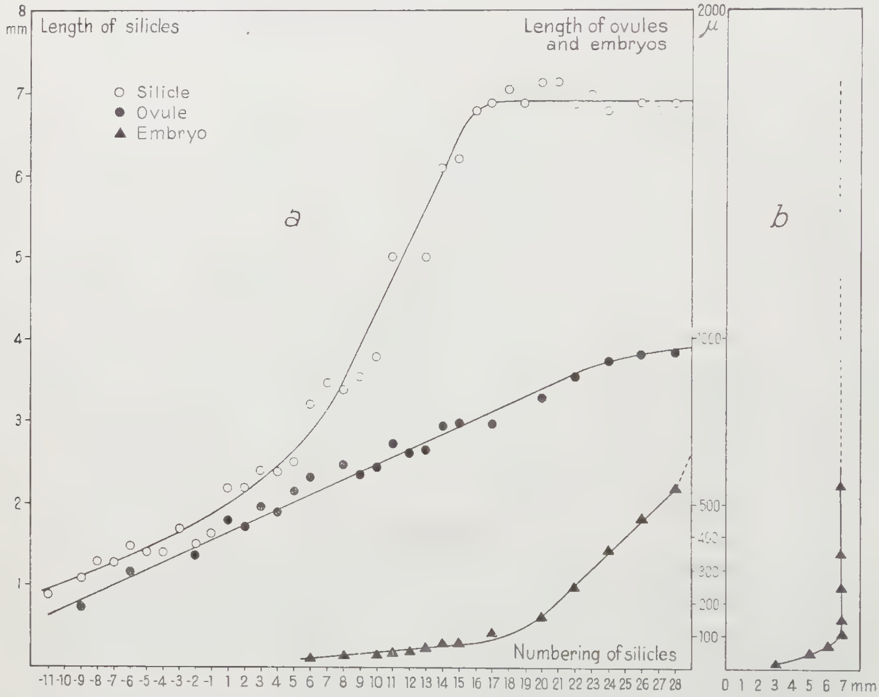


Fig. 3. Explanation see text.

From the data we may conclude that the silicle is the first to grow after pollination, even so that it has already reached mature length when the embryo is still very small, e.g. heart-shaped, as it happens to be in this case; in most other plants the embryos appear to be one stage older. In the course of our investigation we came to the conclusion that our example is representative for young vigorous plants. When the inflorescence passes out of flower, older embryos may be found in the top of the raceme.

§ 4. *The growth of the embryo in the ovule*

As will be clear the embryos cannot be measured without being excised. So an indirect method had to be applied to find out the rate of growth of the embryos in their natural environment. The method was based on our experience, described in the previous section.

A fine plant was selected and the silicles were numbered consecutively from top to base. We planned to measure all embryos, contained in the *odd-numbered* silicles *at a time t*, and the embryos in the *even* silicles *at a time t + 24 hours.*

Now it would be possible to compute the mean lengths of the even silicles also at time *t* by interpolation between the corresponding data from the measurements of the odd silicles at time *t*. This interpolation is facilitated by the arrangement of the silicles, but can only be reliable if applied on a regularly flowering plant, such as the one we had chosen. This plant had been grown in a pot in the open air; before starting the experiment it was placed in a room with a constant temperature of 25° C, and illuminated with a fluorescent tube (Philips T.L.) at a distance of 1.5 m until the end of the test. At a time *t* 30 odd-numbered silicles were removed; each silicle was put in a small numbered tube and kept in a refrigerator until measurement on the same day. Excision and measuring were carried out in a 12 % sucrose solution. 24 hours later we repeated this procedure with the even-numbered silicles. The total number of embryos measured for this experiment came up to ca. 1000.

The results of this experiment are presented in three graphs (figure 4 a, b and c) and will be discussed below.

In some more experiments another method for measuring the growth in the ovule was used. In those cases, the halves of several silicles were removed from the raceme at time *t*, and the other remaining halves 24 hours later; since the two halves of one silicle contain almost equal embryos (cf. section 2), the growth in 24 hours could be found by substraction of the means. The issues thus obtained confirmed the characteristics of the graphs given in figure 4, the discussion of which follows here.

Figure 4a shows the increase in length in 24 hours plotted against the initial length at time *t*. The sagging of the curve, given as a dotted line in the neighbourhood of 500 μ on the abscis is quite probably real. It may be understood as resulting from the fact that during the 24 hours of the experiment, the torpedo-shaped embryos were forced into the walking-stick shape.

From the same data the graph of fig. 4b is derived. Here the abscis is the same as for *a* but the increase in length on the ordinate is expressed as a percentage of the initial length. The reality of the peak at 100—150 μ is highly probable, as it resulted from the other experiments too. Embryos with this initial length start heart-shaped, and during the next 24 hours exhibit mainly longitudinal growth, unlike the preceding globular stages. One may expect that in the latter embryos, growth proceeds with at least equal intensity, but so as to escape for the major part from our longitudinal measurement.

In figure 4c embryo length is plotted against time. The "empirical points" in this graph are derived from figure 4a, as is elucidated there by constructional lines; to begin with the smallest embryo the increase in length of 24 hours is added, which operation is repeated for the sum etc.. The curve drawn through the points, has a strong resemblance to a mathematical sigmoid curve; so we subjected it to a test according to Le Heux (1947), to find out whether T. B. Robertsons growth formula could be applied to it. The formula is:

$$\ln \frac{N}{A—N} = b\,(t—t_1)$$

in which
the variables N length of the embryo in μ
t age of the embryo in hours
and the parameters A maximal length of the embryo: 1760 μ
t age of the embryo when $N = \frac{1}{2}A$, 141 hours
b modulus of the growth

By means of Le Heux' "modulus chart for growth scale" we could establish the value of 1/b at 24 hours. Hence it follows, that in this case the length of the embryo must fit the function:

$$\ln \frac{N}{1760—N} = (1/24)\,(t—141)$$

In figure 4c some points give embryo lengths according to the theoretical suppositions. These "theoretical points" appear almost conterminous with the empirical curve.

B. The endosperm

When the embryos are still immature, their ovules are highly turgescent, so that they release some sap in case they are wounded, e.g. with a needle. This sap can be sucked up into a capillary. When studied under the microscope, it appears to contain spherical nude protoplasts, that constitute the endosperm. The impression of a poorly developed endosperm is confirmed by the microphotographs of sections through ovules (figure 1).

Considering the sap to be the direct medium of the embryo, we tried to gather some facts of its chemical and physico-chemical properties.

§ 5. *Microchemical reactions on the sap from the ovule*

As an implement in this part of the investigation we used a modification of the braking-pipette. The ordinary braking-pipette has been described on page 176 and illustrated in figure 8, but its modified form is provided with an acuminate free tip, making it suitable for pricking into the ovules and sucking up the sap. In most cases, several ovules were drained in sequence, after which the reagent was taken in. Next the point of the capillary was closed by melting it in a micro-flame. If heating was required for the reaction, the same happened at the

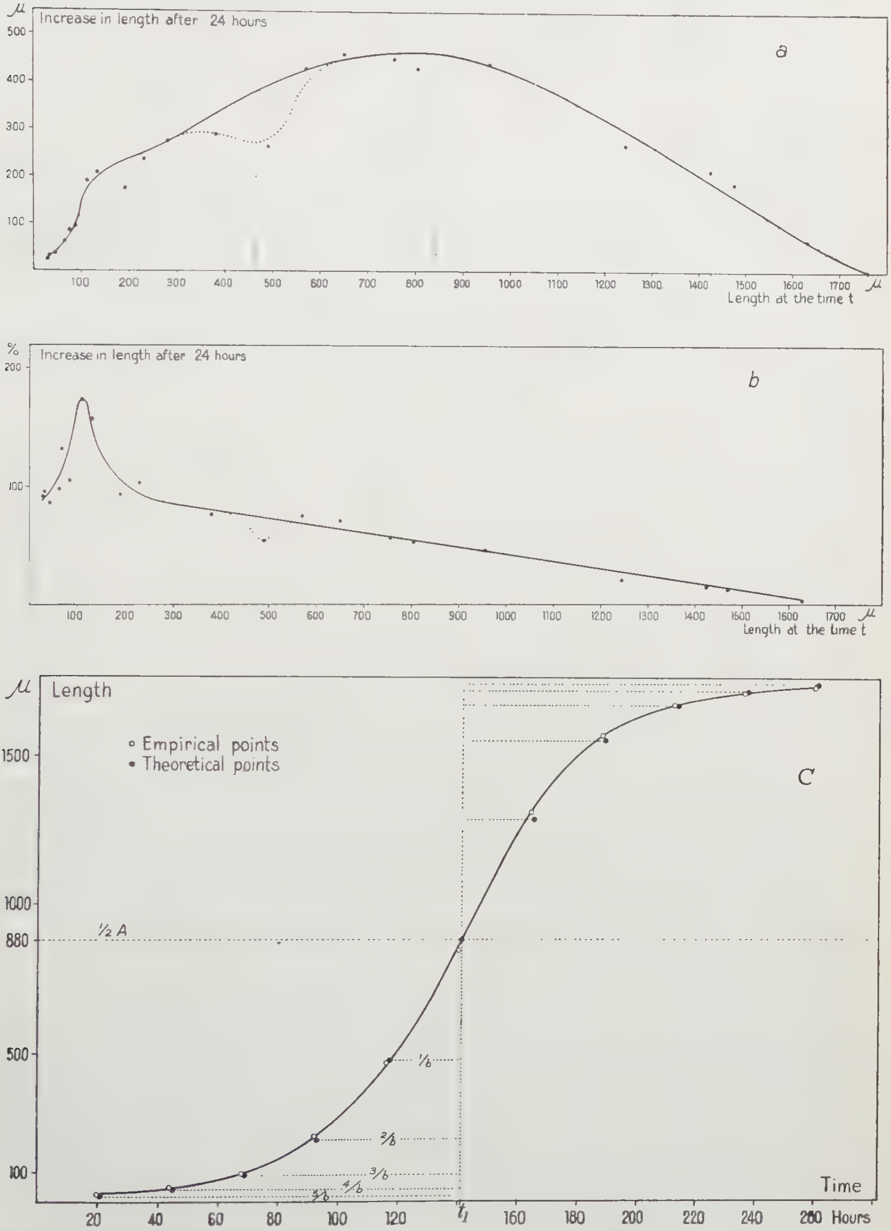


Fig. 4. Explanation see text.

other end, after the capillary had been removed from its holder, heating following in boiling water.

The reactions were done according to Schoorl (1937).

Carbohydrates:

A. Reactions in the pipette.
   1. General reaction on carbohydrates after Molisch: positive when tried on sap from ovules containing 600 μ embryos.
   2. Luffs reaction on reducing monoses: positive when tried on sap from ovules containing resp. 500 and 250 μ embryos.
   3. Barfoeds reaction on reducing monoses: positive when tried on sap from ovules containing resp. 500 μ and 300 μ embryos.

B. Micro-chemical reaction with I–KI solution; in sap from ovules containing 200 μ embryos, small grains of starch could be shown.

Fats:

Whenever tested under the microscope, the sap did not seem to contain any fats.

Amino acids:

Ninhydrin reaction.

1. 4 Ovules containing embryos of 250 μ were drained and the sap was brought on filter paper: the spots gave a positive reaction with ninhydrin.
2. In order to ascertain the presence of free amino acids, a dialysate of the sap from a number of ovules was made as follows: small collodion bags (content 0.5 ml) were filled with 0.4 ml distilled water; one of them, the experimental bag, had the sap from 20 ovules added. All bags were then placed into 1 ml flasks, also filled with distilled water. 24 Hours later, the fluid outside the bags was subjected to the ninhydrin test (by Miss W. Terpstra); the result was positive only for the fluid outside the experimental bag.

§ 6. *pH of the ovular sap*

The principle of the determination of the pH was that of the "Indicator range method" after Small (1928). The quested value is enclosed within a narrow pH-range by a number of indicators, the critical pH of which being exactly known. Again the modified braking pipette was used, by means of which the sap was sucked up first, the indicator following. Then both fluids were blown out of the pipette to a small drop at the end of the capillary. Thus the colour of the drop was quite easily to be noted (cf. table II).

From these data we may conclude that the pH of the sap is about 6.0, both for ovules with small and with larger embryos.

When making these estimations we were struck by the fact that the pH of the integuments appeared to be much lower, as their cells became clearly red in colour when in touch with methyl red as indicator.

TABLE II

The pH of the ovular sap

Indicator	Embryo length in the ovule	Colour	pH
Bromthymol blue	70 μ	yellow	< 6.2
” ”	700 μ	”	< 6.2
Bromcresol purple. . . .	100 μ	yellow-light green	< 6.2
” ”	250 μ	dirty brown	> 5.9
” ”	700 μ	” ”	> 5.9
Diaethyl red	100 μ	yellow-salmon pinky. . .	± 5.9
Methyl red.	50 μ	yellow	> 5.6
” ”	250 μ	”	> 5.6
” ”	700 μ	”	> 5.6
Benzo-azo-naphtyl-amine.	100 μ	yellow	> 4.8
Bromcresol green	100 μ	blue	> 4.4
” ”	300 μ	”	> 4.4

§ 7. *The osmotic value of the ovular sap*

In nature the embryo is embedded in the ovular sap and may be assumed to be in osmotic balance with it. When excised and transferred into a solution, differing in osmotic value, the embryo will become either longer or shorter in dependence. On this principle our method of determining the osmotic value of the sap was based.

Embryos were excised and measured immediately (within 20 seconds). This value was put equal to 100. A series of mannitol solutions of various concentrations had been prepared; after being transferred to one of these solutions, each embryo was measured several times in the course of an hour. The values, gathered by those measurements, were expressed as a percentage of the initial value. In this experiment we used only “torpedoes”, these being most easily prepared and measured.

In figure 5 we resume the results in a diagram, each curve being the average of 4 observations. Though there exists a slight permeability for mannitol, this does not interfere with our conclusion, that 3/8 mol is nearest to the osmotic balance with the embryo; thus the osmotic value of the sap must be isotonic to 3/8 mol (8.4 atm).

The shrinkage of the embryo after a strong initial swelling in pure water indicates the lethal effect of the latter.

The same, somewhat modified method proved to be suitable for the determination of the type of permeability of the embryo too.

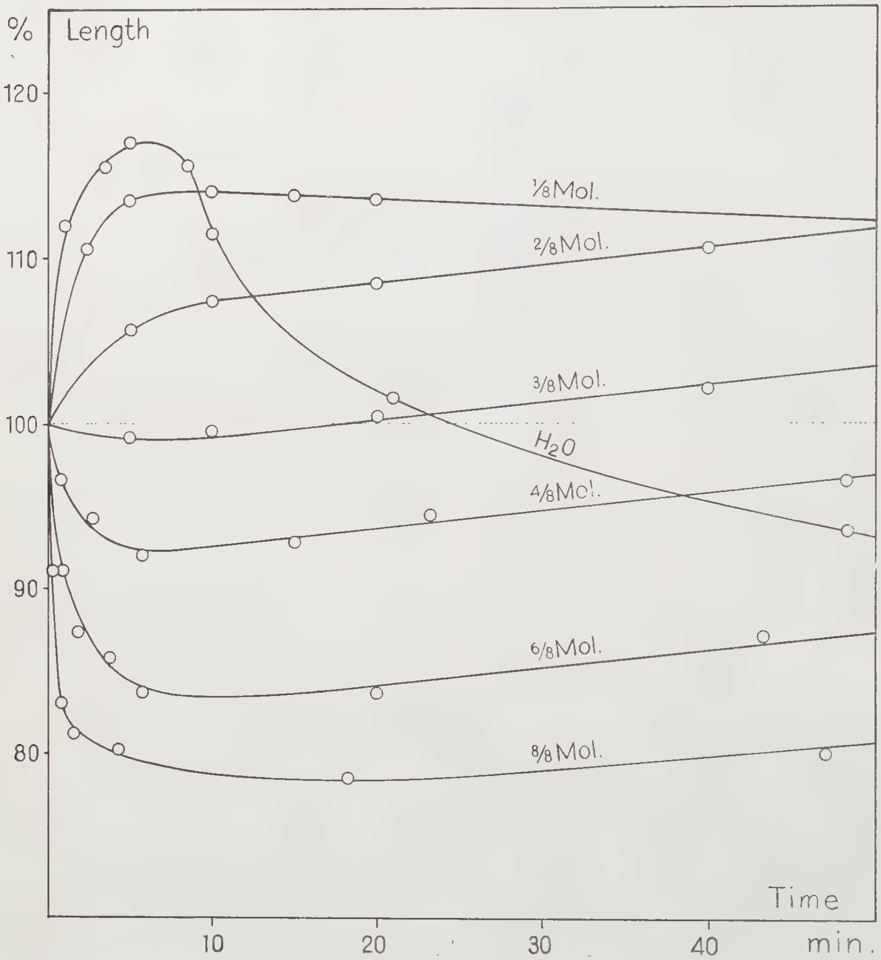


Fig. 5. Explanation see text.

After a 15 minutes stay in ½ mol dextrose, "torpedoes" were transferred to an aequimolar solution of the substance in question. The procentual increase in length after 5 minutes was:

urea	9.6	(with s.e. ± 1.15)
methyl urea	16.1	(,, ,, ± 0.9)
glycerol	16.5	(,, ,, ± 1.5)

So, in respect of permeability, lipophily of the permeating substance seems to predominate over its molecular size.

CHAPTER III

THE PREGERMINAL EMBRYO CULTURE

A. MATERIAL AND METHODS

§ 1. *Material*

1. The plants. In most of the preliminary experiments (chapter III B) plants were used that had grown wild and were collected beforehand. Later *Capsella* plants were grown in the botanical garden of the laboratory, but these had not been selected genetically.
2. Culture cells.
   a. Small VAN TIEGHEM cells: on a slide a glass ring was glued by means of heat resistant resin. The height of the ring was 4 mm and its diameter 20 mm. The cell was covered by a square piece of a slide. Three such cells were kept in a petri dish; thus they were less subtle and more easily sterilized.
   b. Large culture cells, modification of the mentioned VAN TIEGHEM cell, consisting of a small petri dish (diam. 7.5 cm) covered by a square lantern slide (8.2 × 8.2 cm). The centre of this cover glass had been divided into 25 small squares (1 cm^2) by means of glass-pencil lines before sterilization. So one cell could hold 25 hanging culture drops.
   c. Large culture cells, modification of GAUTHERETS cell for the cultivation of a few plant cells (1942). The dimensions of the cell were equal to those of the cell sub *b*. The drops, however, were held between two parallel glass panels. The upper one, the cover glass, was divided in small squares as described sub *b* (cf. figure 6). The lower glass was round and smaller than the petri dish. The two glasses were kept apart by two small pieces of a slide. More details are found in figure 7. In our later experiments we always used this culture cell, because the "hanging drop" caused much trouble in measuring, as the embryos often stuck to the surface and then deviated from the horizontal site.
3. Braking pipette after ZEUTHEN (1943), in use for transferring embryos from one medium to another and for making the drops. The capillary (diam. 1 or 2 mm) was fastened in its holder (a glass tube, diam. 4 mm) by means of resin instead of paraffin, in order to make heat-sterilization possible. Cotton wool was plugged into the holder (figure 8) to prevent infection of the capillary from the operators mouth when in use. A number of pipettes (abt. 25) were kept together in a glass cylinder, in which they had been sterilized before the experiment.
4. Watch glasses, diam. 8 cm, covered by watch glasses, diam. 10 cm.

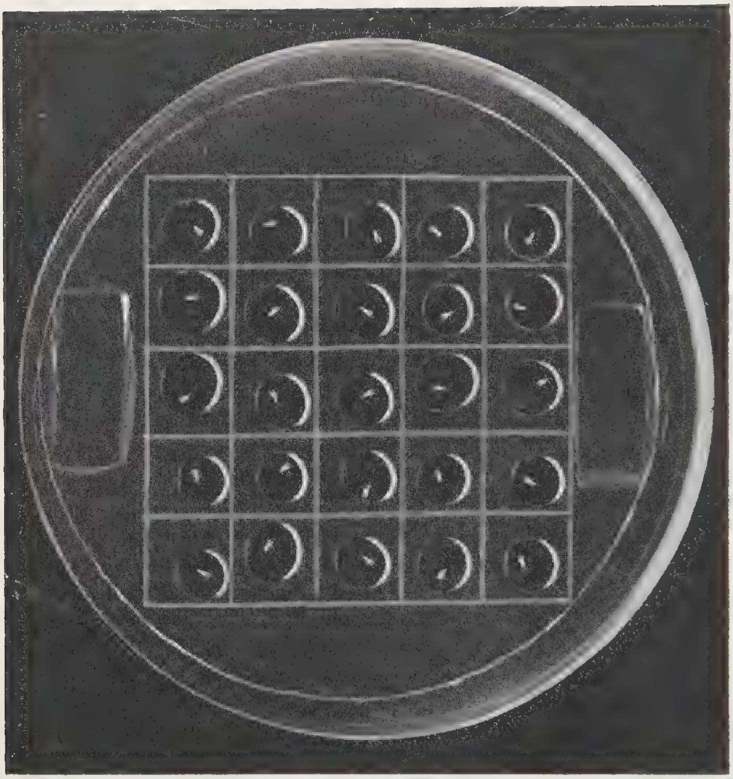


Fig. 6. Explanation see text.

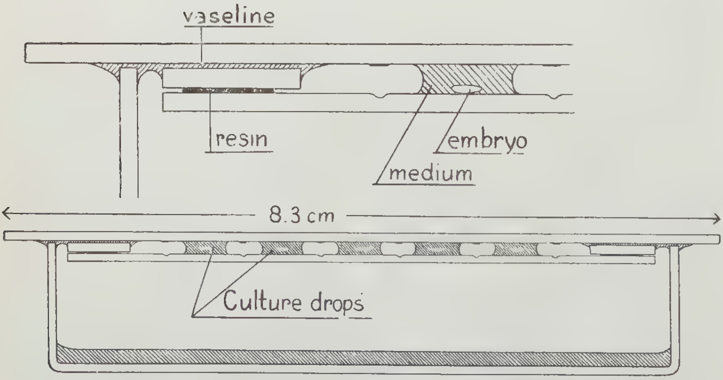


Fig. 7. Explanation see text.

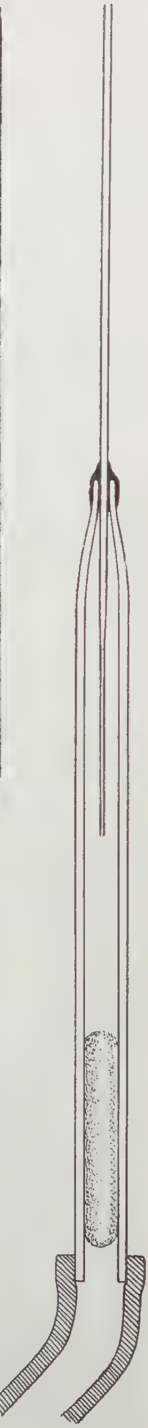


Fig. 8. Explanation see text.

5. Dissecting needles, straight and curved ones.
6. Cover glass tweezers after KÜHNE and CORNET.

§ 2. *Media*

As the finding of a suitable medium was one of the objects of our investigation, the medium was changed again and again, according to the demands of the experiments.

Our starting point was the salt solution of TUKEY (1933), supplied with a number of growth factors after VAN OVERBEEK c.s. (1942). As this solution contains some precipitates of salts that proved inconvenient, we always filtered the salt solution before adding the other components. Another improvement of this first medium was the replacement of KCl by 0.01 mol phosphate buffer after SØRENSEN, which gave the additional advantage, that the pH could be fixed at the desired value.

In all our later experiments we used a salt solution after OLSEN (1950) that did not show any precipitates and contained some trace elements. Also some more growth factors were administered viz. para-aminobenzoic acid, inositol and later lactoflavin, folic acid and biotin in addition.

Sugars were used in a much higher concentration than prescribed by VAN OVERBEEK c.s., viz. at least 80 g per l medium.

In a number of experiments amino acids were added according to their occurrence in the best known plant protein "edestin", as mentioned by TRISTRAM (1949).

Amino acids and growth factors were furnished by HOFFMANN–LA ROCHE, Basel.

The components of the media, and the compositions used, can be found in table III.

§ 3. *Sterilization*

Media in the beginning were sterilized by heating at 100° C during one hour in a KOCH sterilizer. Media containing amino acids, however, became unfavourably altered by this procedure; so we filtered them to free them from germs, in the earlier experiments through a SEITZ-filter, but later on always through glass filters (SCHOTT 11, G 5 auf 3).

Glassware was sterilized, wrapped up in paper, in a muffle at a temperature of 140° C during one hour.

Metal implements (dissecting needles and tweezers) were repeatedly sterilized in the flame when in use.

§ 4. *Excision of the embryos and starting the cultivation*

The first thing to be done was to arrange all implements and appliances in working order on the table. Amongst these was a glass of water in which the cut inflorescences of *Capsella*. A number of silicles, containing embryos in the desired stage, was selected and opened successively. Some practice was required for this operation, as the walls of the silicles had to be removed without severing the ovules from the placenta, in order to prevent their touching any

TABLE III
COMPONENTS OF THE MEDIUM
(* = omitted)

A) 1 Liter 0.01 mol phosphate buffer according to SØRENSEN.

B) Salts:

	1) TUKEY (1933)	2) OLSEN (1950) modified
$CaSO_4$	185 mg	
$Ca_3(PO_4)_2$	185 ,,	
$MgSO_4.7H_2O$	185 ,,	101 mg
$Fe_3(PO_4)_2$	185 ,,	
*KCl	680 ,,	
KNO_3	135 ,,	149 mg
$Ca(NO_3)_2.4H_2O$	—	168 ,,
*KH_2PO_4	—	23 ,,
$MnSO_4.4H_2O$	—	0.4 ,,
H_3BO_3	—	0.4 ,,
$ZnSO_4.7H_2O$	—	0.2 ,,
$CuSO_4.5H_2O$	—	0.1 ,,
$(NH_4)_2MoO_4$	—	0.05 ,,
1 % Ferric citrate	—	5 cc

C) Sucrose: 1) 80 gm 2) 120 gm 3) 180 gm

D) Growth factors:

		VAN OVERBEEK (1942)	extra
1)	*Ascorbic acid	20 mg	—
	*Glycine	3 ,,	—
	Thiamin	0.15 ,,	—
	Nicotinic acid	1 ,,	—
	Pyridoxin	0.2 ,,	—
	*Adenine	0.2 ,,	—
	Ca pantothenate	0.2 ,,	—
	Inositol	—	0.5 mg
	p-Aminobenzoic acid	—	0.5 ,,
2)	Riboflavin	—	0.1 mg
	Folic acid	—	0.01 ,,
	Biotin	—	0.0004 ,,

E) Amino acids: 1 gram in accordance with the composition of edestin (Tristram, 1949).

Alanine	4.31 %	Lysine	2.4 %
Valine	5.7 %	Aspartic acid	12.0 %
Leucine	4.7 %	Glutamic acid	20.7 %
Iso-leucine	7.5 %	Amide NH_3	2.15 %
Proline	4.25 %	Serine	6.3 %
Phenylalanine	5.45 %	Threonine	3.85 %
Half cystine	0.93 %	Tyrosine	4.34 %
Cysteine	0.50 %	Tryptophane	1.48 %
Arginine	16.7 %	Methionine	2.4 %
Histidine	2.9 %		

MEDIUM I: combination of A, B 1, C 1, D 1.
,, II: ,, ,, A, B 1, C 1 or C 2.
,, III: ,, ,, A, B 1, C 2, E.
,, IV: ,, ,, A, B 2, C 2 or C 3, (D 1 + 2), E.

unsterile parts. This was achieved by tearing the walls down from the ribs by means of a pair of coverglass tweezers after Kühne. The remainder of the silicle, including the ovules, was then placed in a sterilized watch glass; then the ovules were pulled off from the placenta with sterilized needles under a dissecting microscope. Another watch glass with 5 ml sterile medium, covered by a larger watch glass, used to be ready for the receipt of the ovules. The excision of the embryos followed by cutting a gap in the top of the ovule and exerting a slight pressure on its base near the micropyle. To prevent infection during these manipulations, the operators head, except the eyes, was covered by a sterile cloth, as is usual in surgery.

About 20 embryos could be excised within ten minutes. By means of a braking pipette we then brought them to a second, and from this to a third covered watch glass with medium in order to clean them from adhering rests of endosperm and from eventual contaminations.

These operations having been repeated for a number of silicles, the culture was started. Though one person may be able to perform this part of the technique, sterility was served best by a rapid sequence of manipulations as achieved by a team of two persons. One of them made drops of about 10 mm^3 on the underside of the cover glass that had been clipped between coverglass tweezers after Cornet; the other person introduced the embryos into the drops with the braking pipette. Then the coverglass was laid over the cell, the brim of which had been lined with vaselin. Also a bottom drop of nutrient solution was inserted in the moist chamber in order to prevent evaporation and change of concentration of the hanging culture drop.

When using the large culture cells, we could omit the repetition of several manipulations, which meant a lot of time saved.

§ 5. *General culture conditions*

After sealing the culture cells, they were always incubated in the same dark room with a constant temperature of 25° C. Measuring was done in the same room, in orange light, as in use in experiments on growth (Orange filter; Schott OG 2).

In some cases we used other temperatures or light during the cultivation. This will be mentioned in the sections in question.

§ 6. *Growth measurements*

Cultivated embryos are always straight. Their lengths were determined with an ocular micrometer. The measuring can be warranted correct to half a scale unit (the usual unit was 12.8 μ; small or very big embryos were measured with units being 8.8 μ and 24.3 μ resp.).

In most cases the growth is expressed as the procentual increase of the initial length (length of first measurement). By means of a t test (Fisher, 1946) we checked, whether the differences in growth between the various series were significant. Each experiment included a control series. In the tables the standard error is marked: ±.

B. PRELIMINARY EXPERIMENTS

The experiments, that will be reported under this heading, are short preambulary tests as to a number of general milieu requirements. They were carried out at the start of our investigation.

It soon became clear, that the nutrient solution we used (VAN OVERBEEK c.s. 1942) did not meet the needs of experiments of longer duration. The administration of amino acids proved to be a considerable improvement (section 12).

The composition of the numbered media can be found in table III.

§ 7. *The growth of embryos, varying in initial length*

As it is quite impossible to gather a sufficient number of exactly equal embryos for an experiment, we first had to find out whether embryos, varying in initial length, would yield the same relative growth.

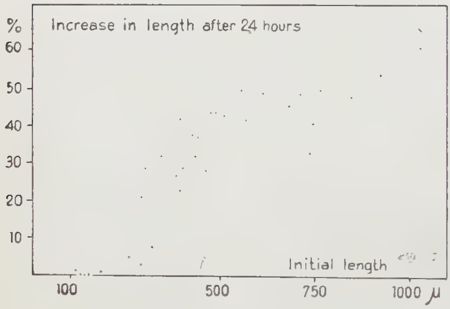


Fig. 9. Explanation see text.

To this end we started the culture of 60 embryos from 100—900 μ. Conditions: medium I; pH 6.6; darkness; temp. 25° C. Figure 9 shows the growth in 24 hours in dependence on the initial length, as a number of points, making a diagram. On the whole, there certainly appears to be a correlation between the growth rate and the initial length; on closer examination however the differences in the growth of embryos, initially between 500 μ and 750 μ seem to be caused by chance. The data on these embryos are given in table IV. From these a correlation coefficient *r* could be calculated. The result was: $r = -0.304$, with $0.3 > P > 0.2$, which proved that this variability is merely incidental. Therefore, we further took care not to surpass the limits of 500 μ and 750 μ.

Another fact, that can be learned from table IV is the strong decrease in growth percentage in the course of some days. The possibility that a change in the medium did cause this decrease, had to be examined. For that purpose we made two experiments.

In the first experiment 6 out of 13 cultivated embryos got their medium replaced by a fresh drop after 48 hours. As is shown in figure 10 the decrease in the growth in this case is essentially the same as that of the control embryos, the medium of which had not been renewed.

In the second experiment freshly excised embryos were inoculated

TABLE IV

The growth of embryos from the group of 500—750 μ during 4 days in medium I, pH 6.6; dark; temp. 25° C.

Embryo-number	Initial size in μ	Procentual increase in length				
		1st day	2nd day	3rd day	4th day	total 4 days
1	510	43	25	3	3	89
2	514	35	21	9	4	84
3	528	37	26	7	5	93
4	537	44	18	6	3	85
5	537	44	20	5	5	90
6	546	50	19	—	—	—
7	564	39	21	11	7	99
8	564	42	21	5	3	86
9	610	49	22	—	—	97
10	683	46	20	8	4	97
11	701	49	15	7	5	92
12	719	33	27	6	6	90
13	719	40	22	5	4	87
14	719	39	21	8	4	90
15	728	33	16	11	4	77
16	742	41	24	8	8	105
Mean:		41.5	21.1	7	4.6	90.7
Standard error		1.35				1.7
Standard deviation: . . .		5.4				6.3

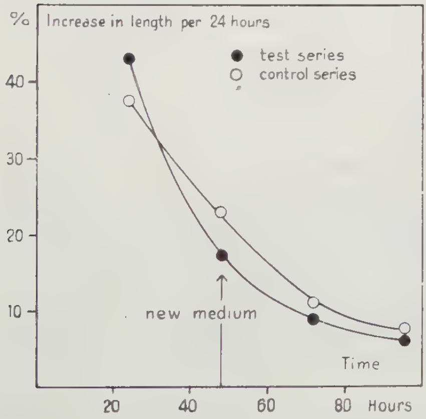


Fig. 10. Explanation see text.

into the drops, in which other embryos (series 1) had already been cultivated for 4 days. These embryos grew only 8 % during the last day; yet the new embryos (series 2), started growing in the same drops as if the medium had been fresh (cf. table V).

The results of these experiments justify the conclusion, that the growth of cultivated embryos was limited, if not yet on the first day, at least during the next days, by the shortage of one or more nutritional factors, lacking in the medium, and gradually getting exhausted in the store of the embryo.

TABLE V

The growth of two series of embryos; series 2 has grown in drops, in which the embryos of series 1 had been cultivated for 4 days, the growth rate of which had decreased to 8 %. Medium I with 120 gm sucrose / liter; pH 6.6; darkness; temp. 25 C.

Series	Number of embryos	Mean value of initial length	% Growth after 24 hours
1	14	628 μ	43.5
2	10	595 μ	44.7

§ 8. *Influence of the pH*

In a series of experiments the influence of the pH was also tested. The nutrient used was medium I; the pH was: 4, 5.4, 6.6, and 7.5. Its value was determined immediately after inoculation on the remainder of the medium with a quinhydrone electrode.

Table VI shows the results for embryos with an initial length between 500 μ and 750 μ. From the data of the first day it is clear that from pH 6 down the embryos do not thrive very well; a value below pH 5 appears to be even unfavourable. However, when considering the total growth in four days, we must conclude that the growth rate decreased in all cases independent of the pH of the medium from the first day on, but so as to yield a total growth of about 90—100 %. This again is in favour of our view on the limitation of the growth by nutritional factors, mentioned in the previous section.

TABLE VI

The growth of embryos from the group of 500—750 μ at different pH. Medium I, darkness, temp. 25° C.

pH	Number of embryos	Mean value of initial length	% Growth after 24 hours	% Growth after 96 hours
4*	16	590 μ	23 ± 2.7	98
5.4	15	597 μ	35.3 ± 1.7	93
6.6	16	620 μ	41.5 ± 1.35	91 ± 1.7
7.5	11	570 μ	43 ± 1.3	90

* 20 % of the embryos died.

§ 9. *Influence of the temperature*

A great number of embryos was cultivated for the temperature test. They were distributed over five incubators with temperatures of resp. 21°, 25°, 30°, 35° and 40° C. The nutrient was medium I; pH 5.8. The results show the optimum curve of figure 11.

Again the possibility that the growth rate is mastered by general —non nutritional—milieu factors during the first 24 hours, is confirmed. In previous sections we stated, that this is not the case when considering the total growth in 96 hrs. The only way to increase this total must be the addition of nutritional factors unknown as yet. So we may have found a criterion for the identification of these factors.

§ 10. *Influence of light*

Freshly excised embryos are green when over 250 μ, and not yet mature. Cultivation without light causes the green colour to disappear; the embryos become white within the course of some days.

The main difficulty of cultivation in light was the necessity of maintaining the same constant temperature for the lighted and for the control (dark) series. So we put the control series in a lightproof zinc box on top of which the light-series was placed. Over this a lamp was installed, the infra red of which being mostly absorbed by a water filter. The whole set was placed in a room with constant temperature.

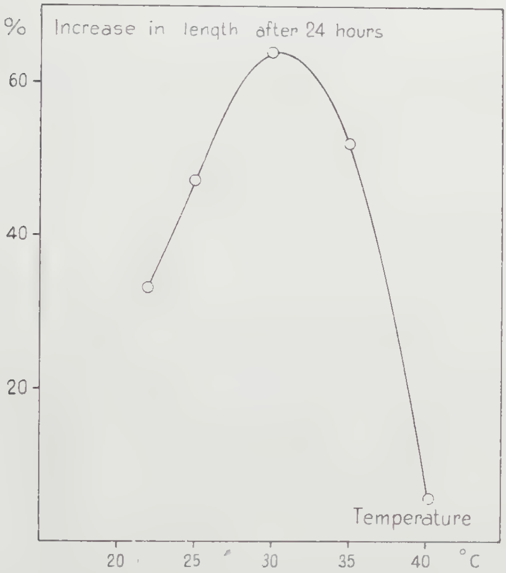


Fig. 11. Explanation see text.

In our first experiment we used a high-pressure-mercury lamp (Philips Philora HP 75 W) of a light-intensity of ± 500 Lux near the culture cells. Table VII shows the results. Though light does not seem to have any influence, we continued the cultivation in the dark in all experiments to follow.

At the end of our investigations the experiment was repeated. We then knew that the growth is far better in a medium with glutamine

TABLE VII

The growth of embryos in light and darkness. Medium I, pH 6.7; temp. 25° C.

	Number of embryos	Mean value of initial length	% Growth after 48 hours
light. . .	17	504 μ	55 ± 2.4
dark. . .	18	491 μ	54.3 ± 2.9

added to it (Chapter III C). In this case there appeared to be a slight inhibiting action of light, but only after 4 days its significance could be shown (cf. table VIII). Tropistic phenomena were not noticed.

The light source was a Philips T.L. tube; the intensity near the culture cells was ± 450 Lux.

TABLE VIII

The growth of embryos in light and darkness. Medium IV with 120 gr. sucrose and 760 mgr. glutamin per liter. pH 6.1; temp. 25° C.

	Number of embryos	Mean value of init. length	% Growth 24 hours	% Growth 48 hours	% Growth 96 hours
light. . .	11	446 μ	82.9 ± 1.3	165 ± 3.4	297 ± 8
dark. . .	15	428 μ	87.5 ± 1.8	175 ± 2.75	341 ± 5.6

§ 11. *The influence of various sources of carbon*

Among our first preambulary experiments was a test as to the most favourable source of carbon. In a number of one-day-cultures we tried several substances, mainly sugars, viz.: sucrose, maltose, dextrose, dextrose + fructose, raffinose, lactose, mannitol and glycerol. Isotonic concentrations were used in order to get comparable results. We feared that errors might be caused by heat sterilization of the media; so we did not sterilize all of them, and moreover we added some unsterilized control series. Sterilization proved to have no effect (cf. table IX).

TABLE IX

The growth of embryos in medium II, with 8 % sucrose, and aequimolar substitutes; pH 6.6 or 6.7; darkness; temp. 25° C.

C-source	gr./L	Sterilised			Not sterilised		
		Number of embr.	Mean value of init. length	% Growth 24 hrs.	Number of embr.	Mean value of init. length	% Growth 24 hrs.
sucrose	80	12	466 μ	48	9	566 μ	48 ± 1.6
maltose	80				8	564 μ	40 ± 2.5
dextrose	45.8	10	460 μ	30			
dextrose	45.8				8	571 μ	29 ± 1.4
fructose	44.2						
raffinose	139				12	550 μ	17
lactose	80	9	449 μ	6	9	550 μ	7
mannitol	42.6	6	480 μ	11.5			
glycerol	21.5	10	550 μ				

Sucrose turned out to be the most favourable carbon source for growth, though it is not certain that maltose does not match it; the t test gave for the difference: P = 2 %.

On the other hand it is clear that dextrose is less suitable. No better results were obtained by mixing equal parts of isotonic solutions of dextrose and fructose. Dormer and Street (1949), who cultivated tomato roots, met with the same phenomena and demonstrated, that they could not be accounted for by possible impurity of the sugars.

Later, after glutamic acid had turned out to be a rather good source of nitrogen (Chapter III C), we made a closer examination of the difference between sucrose and dextrose by means of concentration series of both sugars (table X). The higher concentrations of both sugars did not yield any difference in this more suitable medium, but in lower concentrations sucrose still appeared to be a better carbon source.

TABLE X

The growth of embryos in media with different sugar-concentrations, in the presence of glutamic acid. Medium II, with 1.54 gr/l glutamic acid; pH 5.8; darkness; temp. 25° C

C-source	Number of embryos in each series	% growth after 24 hours				
		0.1 mol	0.2 mol	0.3 mol	0.4 mol	0.5 mol
sucrose	16	60 ± 1.33	71 ± 2.0	64 ± 1.27	67 ± 1.96	
dextrose	18		46 ± 1.41	64 ± 1.15	64 ± 0.97	57 ± 1.85

§ 12. *The limiting nutritional factors*

When the embryos are mature their cells are crowded with aleuron grains that give evidence of an intensive protein synthesis during the development. The materials for this synthesis are quite probably obtained as amino acids from the ovular sap, in which we could show their presence (cf. p. 172.).

In all preambulary experiments the medium contained nitrate as the sole nitrogen source; so the most plausible inference was that amino acids would be the growth limiting factor.

Our first check of this hypothesis was the administration of casein hydrolysate, added to medium II in a series of concentrations. As we explained in section 9, the total growth in four days should be the criterion. The results confirm our view (cf. table XI). A series with non-hydrolysated casein did not prevail over the blank control series.

TABLE XI

The growth of embryos (500—750 μ) on medium II with different concentrations of hydrolysate of casein; pH 6.7; darkness; temp. 25° C.

Added to 100 ml medium		Number of embr.	% Growth after 48 hrs.	% Growth after 96 hrs.
Control.		15	51.8 ± 1.1	71.8 ± 1.8
Casein	100 mg	15	52.7 ± 2.3	
± 20 % solution of hydrolysate of casein	0.089 ml	15	79.6 ± 4.7	
	0.196 ml	14	92.3 ± 3.3	
	0.382 ml	14	109.4 ± 4.4	174.4 ± 5
	0.734 ml	8	116.0 ± 3.9	
	1.344 ml	13	99.5 ± 5.6	145.5 ± 7.9

Sterilization of the media containing casein hydrolysate was done by Seitz filtration, as autoclaving of such media proved inadequate; precipitates appeared and an inhibiting effect resulted.

A more profound analysis of various sources of nitrogen is given in the following pages.

C. THE ANALYSIS OF THE SOURCE OF NITROGEN

§ 13. *Administration of the complete mixture of amino acids*

After detecting the favourable effect of casein hydrolysate, we obviously had to continue our research by testing the effect of pure amino acids, a complete set of them in the first place. As to the mutual proportion of the amino acids in the mixture, it seemed the best thing to imitate the composition of globulins, present in the mature seeds. Of most plant globulins, however, the composition is not exactly known; so we had to content ourselves with the data about edestin, this being the only well-known plant globulin. In table III its composition is given. A striking feature of it is the high percentage of glutamic acid, aspartic acid and arginine. There are indications that many plant globulins show the same characteristics; on the other hand it is known that the globulins of the various plant families differ to a certain degree (LUGG, 1949).

The amino acids tyrosine, cysteine and cystine are hard to solve. Therefore they weer solved apart from the others in a little drop of concentrated hydrochloric acid. Sterilization of the media from now on was always done by filtration through glass filters (Jena, G5 auf 3).

Figure 12 gives the growth of embryos, "torpedoes", initially between 500 μ and 750 μ long, in dependence on the concentration of the amino acids. The measure of the latter is expressed in mg per 100 ml; the composition of the mixture in all cases is that of edestin. The graph shows, that the amino acids limit the growth rate in the lower concentrations. The concentration required for unlimited growth appears to increase with the duration of the experiment. A culture period of four days requires about 50 mg per 100 ml.

The embryos show a similar dependence on amino acids, increasing with increasing culture time, as stated for the unknown nutritional factors in the experiments without amino acids.

Henceforth media always got either 106 mg amino acids (complying with the composition of edestin, cf. table III) per 100 ml or other nitrogen containing substances. In the latter case we took care to maintain nitrogen aequivalence (106 mg amino acids contain 14.63 mg N).

Our first experiment in the spring of 1951 served to find out whether nitrogen, supplied as an organic ammonium-compound viz. ammonium lactate, could match the effect of amino acids. The growth proved to be abnormally high, both in the control and in the experimental series, probably because of better storage in the embryos early in the season, but the difference between the two series left no doubt as to the issue of the experiment (cf. table XII). Ammonium lactate can by no means replace the amino acids.

TABLE XII

Ammonium lactate and the complete mixture of amino acids (edestin) as N-source. Medium IV (12 % sucr.); pH 5.75; darkness; temp. 25° C.

N-source	Number of embryos	Mean value of initial length	% Growth after 96 hours
Amino acids	15	abt. 600 μ	289 ± 10.5
NH_4-lactate	14	abt. 600 μ	174 ± 2.8

TABLE XIII

Glutamic acid and the complete mixture of amino acids (edestin) as N-source. Medium IV (12 % sucrose); pH 6.7; darkness; temp. 25° C.

N-source	Number of embryos	Mean value of initial length	% Growth after 96 hours
Amino acids.	26	abt. 600 μ	209 ± 3.3
Glutamic acid	36	abt. 600 μ	185 ± 4.6

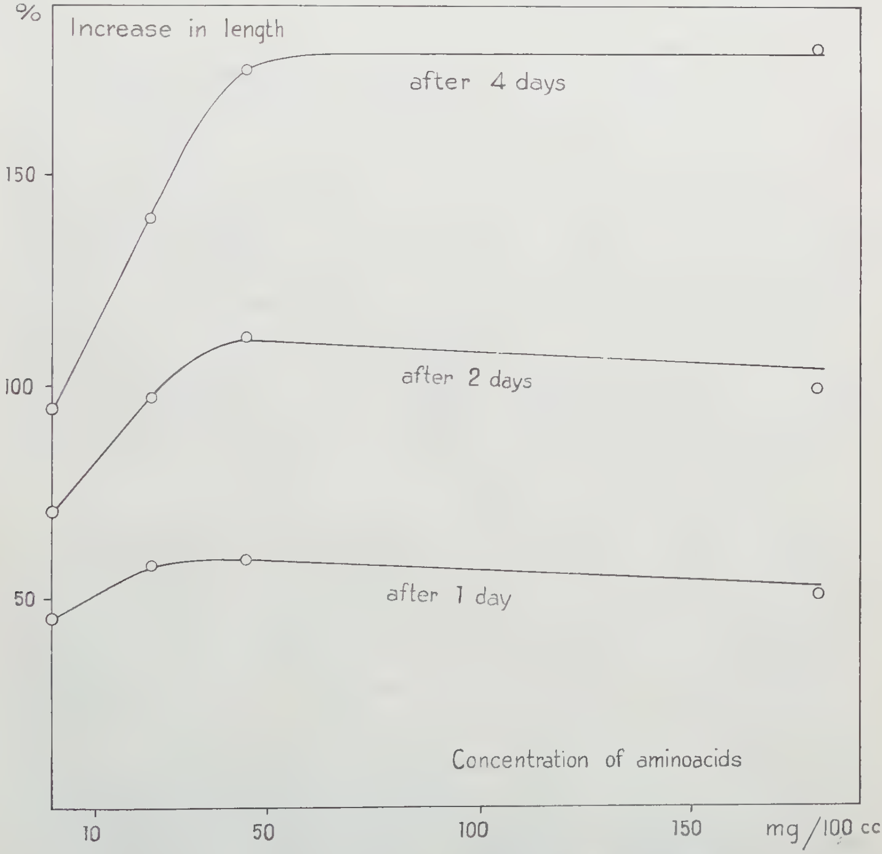


Fig. 12. The growth of "torpedoes" on medium III with different concentrations of amino acids (composition according to edestin); pH resp. 7.2, 6.94, 6.94, 6.94; darkness; temperature 25° C.

The next problem we wanted to solve was the possibility of replacing the complete set of amino acids by glutamic acid alone, which is supposed to take a key position and to play an important part in transaminations. The results of these experiments were hardly conclusive; a significant, though slight difference is shown in the case of table XIII, in which the glutamic acid series falls behind the amino acid series. As these results were not remarkable, we decided to continue the analysis with young heart-shaped embryos, in the hope that these would show a more pronounced heterotrophy in this respect.

§ 14. *The influence of various single amino acids in the culture of heart-shaped embryos*

For the cultivation of heart-shaped embryos the same conditions held as for that of torpedoes, except the sugar concentration that has to be increased up to 18 per cent (0,526 mol). After some experimentation we switched over to this concentration because some phenomena had indicated 12 per cent to be hypotonic in the case of heart-shaped embryos before.

Our first experiment consisted of two series, one of which was supplied with a complete set of amino acids, whereas the other one got only glutamine *. The reason why we preferred glutamine over glutamic acid is the difficulty of adjusting the pH when using glutamic acid; in the case of glutamine the normal phosphate buffer can be used, while glutamic acid media require neutralization by alkali in concentrations that might do harm to the delicate embryos. The results of the experiment are given in table XIV. They show a considerable, significant difference in favour of glutamine, an issue that could repeatedly be reproduced.

Seemingly this result is at variance with that referred to in the preceding section, but it should be born in mind that we then used glutamic acid and, consequently, had to add a considerable amount of alkali. In some cases we used glutamine also for torpedoes which always resulted in an unusually high growth rate (cf. e.g. table VIII).

TABLE XIV

Glutamine and the complete mixture of amino acids (edestin) as N-source. Medium IV (18 $^0/_0$ sucrose); pH 6.2; darkness; temp. 25° C. Experiment with heart-shaped embryos

N-source	Number of embryos	Mean value of initial length	% Growth after 96 hours
Amino acids.	35	abt. 140 μ	225 ± 5.5
Glutamine.	42	abt. 140 μ	295 ± 7

After these experiments it was apparent that the effectiveness of various amino acids is different with respect to their growth promoting activity in the embryo culture of *Capsella*. It seemed quite possible even that one or some of them act as inhibitors. In this regard we especially had suspicion of tyrosine, because of its molecular structure, which holds the possibility of "auxin" activity, according to the theoretical considerations of Veldstra (1949). Indole-3-acetic acid had then already turned out to inhibit growth (cf. chapter III D). Our surmise was checked by cultivating embryos in a medium that contained, apart from glutamine, 10 mg tyrosine per 100 ml. In this medium growth was much lower indeed (cf. table XV). If tryptophane or phenylalanine, which are somewhat similar in structural features, were administered instead of tyrosine no significant difference with the control series (glutamine alone) could be stated.

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* We thank Dr F. van Walraven, scientific agent for the Netherlands of Hoffmann–La Roche & Co, Basel, for his kind help in procuring us glutamine.

TABLE XV

Glutamine, glutamine + tyrosine and asparagine as N-source. Medium IV (18 % sucrose); pH 6.2; darkness; temp. 25° C.

N-source	Number of embryos	Mean value of initial length	% Growth after 96 hours
Glutamine.	25	abt. 170 μ	315 ± 11
Glutamine + tyrosine.	13	abt. 170 μ	167 ± 10.5
Asparagine	28	abt. 170 μ	58 ± 3.5

Another point of interest was the question whether the beneficial influence of glutamine is exceptional for this very amino acid, a view, endorsed by recognized biochemical arguments. For a highly important key position as a link between carbohydrate- and protein-metabolism is ascribed to glutamic acid. A similar function, however, is attributed to aspartic acid as well and to some degree also to alanine (Braunstein, 1947).

In conformity with this view alanine proved to cause a considerable growth, though its mean value was much lower than that of the glutamine series (table XVI). The homologous compound glycine, however, could by no means satisfy as a source of nitrogen: one third of the embryos died in it within four days, while the rest did not grow more than 40 per cent in total.

TABLE XVI

Glutamine, complete amino acid mixture and alanine as N-source. Medium IV (18 % sucrose); pH 6.2; darkness; temp. 25° C.

N-source	Number of embryos	Mean value of initial length	% Growth after 96 hours
Glutamine.	17	abt. 170 μ	298 ± 9.0
Amino acids	27	abt. 170 μ	237 ± 5.95
Alanine	15	abt. 170 μ	209 ± 3.0

When administering asparagine, remarkable results were obtained. The growth rate in a medium with this amino acid was surprisingly low (cf. table XV). Yet the embryos did not die, as they did in a glycine medium. This effect was obtained with crystalline asparagine of different origin. So the unexpected phenomenon cannot be ascribed to impurities of the preparation. Apparently asparagine, unlike glutamine, cannot play a crucial part in the protein synthesis of *Capsella* embryos. A different pattern of metabolism came into action as became clear already after 24 hours of cultivation when comparing embryos in the glutamine and the asparagine series: even the smallest embryos (150 μ) of the asparagine series had formed much starch in their cells as early as that, whereas, in the glutamine series starch could scarcely be noticed. In the discussion (p. 195) we will go deeper into the matter.

D. The influence of ergones

§ 15. *Bios factors*

To check the influence of growth factors we carried out a number of experiments, each comprising a control series and some series in which several bios factors were added, the richest medium containing nine of the best known factors (cf. table III). In all cases the results were negative, in the early experiments made before the necessity of amino acids in the medium had been shown, as well as in the later ones, when an adequate source of nitrogen was present. Tables XVII and XVIII may suffice in illustrating the facts; the first comprises data about "torpedoes", the latter about heart-shaped embryos.

TABLE XVII

Bios-factors and purine-derivates added to Medium IV (12 % sucrose); pH 6.7; darkness; temp. 25° C.

Ergones	Number of embryos	Mean value of initial length	% Growth after 96 hours
——	26	abt. 600 μ	209 ± 3.3
Bios-factors	17	abt. 600 μ	208
Purine-derivates . . .	22	abt. 600 μ	212

These negative results are not at variance with the findings of other authors as will be shown in the discussion (p. 195).

Many experiments were performed with media, lacking growth factors; yet such cultures yielded viable embryos.

TABLE XVIII

Bios-factors and adenosine-3-phosporic acid to Medium IV (with glutamine as N-source and 18 % sucr.) pH 6.2; darkness; temp. 25° C.

Ergones	Number of embryos	Mean value of initial length	% Growth after 96 hours
——	21	175 μ	325 ± 7.1
Bios-factors	13	190 μ	316 ± 12.5
Adenosine-3-phosphoric acid . .	25	170 μ	326 ± 5.8

PLATE VI

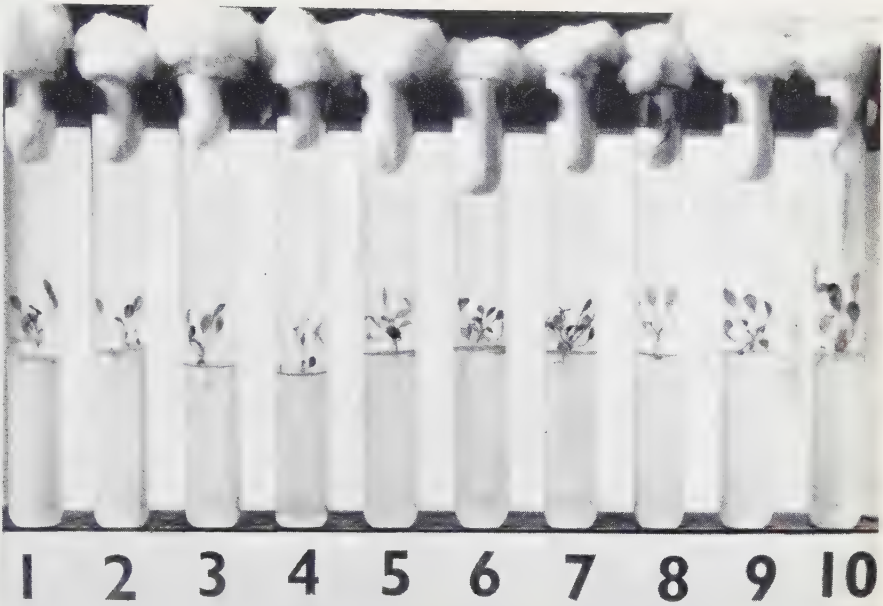

Fig. 13. Explanation see text.

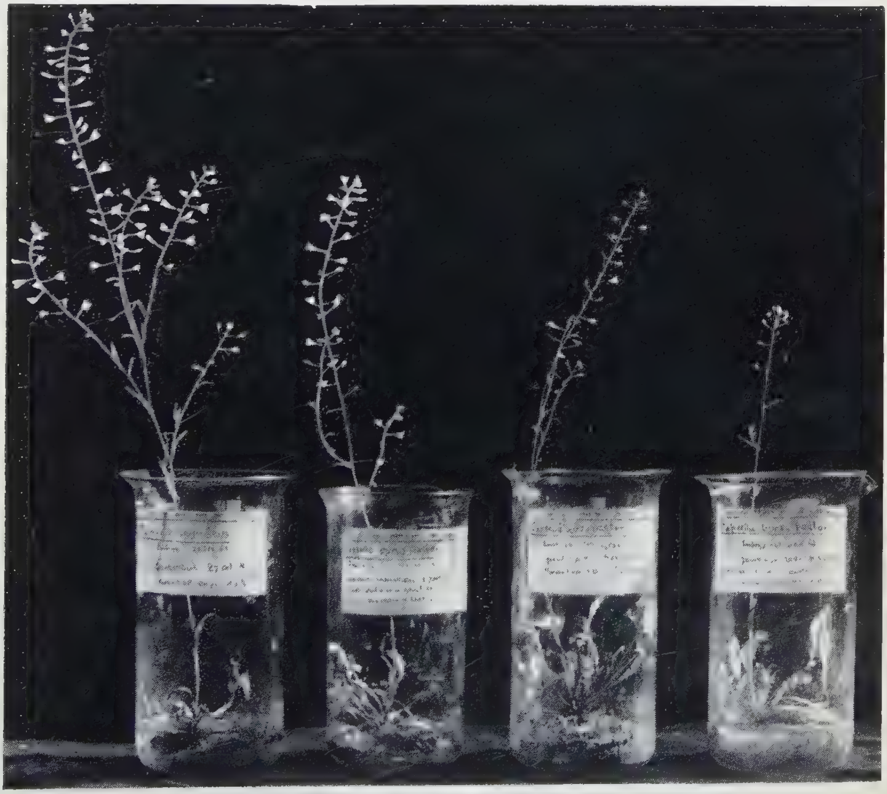

Fig. 14. Explanation see text.

§ 16. *Purine derivatives*

The tables XVII and XVIII give also the results of some series of embryo cultures, the media of which contained purine derivatives. When preparing the medium, our nucleic acid, however, did not solve completely. The series of table XVII had nucleic acid and adenosine-3-phosphoric acid added, each of them in a concentration of 10 p.p.m.; that of table XVIII only adenosine-3-phosphoric acid in the same concentration. Also these experiments yielded negative results, which will be discussed below (p. 196).

§ 17. *Hetero-auxin*

In connection with the multifarious activities, accredited to indole-3-acetic acid, we decided to try this substance in our embryo cultures too. Two experiments were made, from which we could gather the data given in table XIX. In the last column the growth rates are expressed as percentages of the controls. An influence is obvious and becomes significant in the concentrations 10, 1 and 0.001 p.p.m. The effect is inhibitory in concentrations over 0.1 p.p.m. and promoting in the lower concentrations. The influence, however, is rather weak, too weak to justify any conclusion for a longer duration of the experiment, as the variation became too large after some days. In the discussion we will also consider these results (p. 196).

TABLE XIX

Two experiments on the influence of indole acetic acid on the procentual growth of "torpedoes" in 24 hours. Medium IV (12 % sucrose; exp. A with glutamine as N-source, exp. B with complete mixture of amino acids); pH 6.2; darkness; temp. 25° C.

Conc. I.A.A. p.p.m.	Number of embr.		% Growth		Difference of means and its s.e.	P in %	Growth in % of control
	A	B	A	B			
0	28	15	68.6 ± 1.23	57.9 ± 1.73			100
10	27		62.2 ± 1.2		4.2 ± 1.7	1—2	90.7
1		24		53.2 ± 1.3	4.7 ± 2.15	2—5	91.9
0.1	22		68.3 ± 1.95		0.3 ± 2.5		99.6
0.01		20		60.1 ± 0.86	2.2 ± 1.95		103.8
0.001	28		72.6 ± 1.4		4.0 ± 1.85	2—5	107
0.0001		12		62.6 ± 2.2	4.7 ± 2.8		108.1

CHAPTER IV

THE POSTGERMINAL EMBRYO CULTURE

Actually a successful postgerminal culture is the best proof of the viability of the cultivated embryos. Therefore we also gave some attention to this kind of culture, though our experiments did not cover the field systematically.

In the culture cells the embryos never spontaneously started germination; so "künstliche Frühgeburt" was out of the question (cf. page 160 and 162) and the growth we measured certainly was not cell-elongation but embryonic growth. The most likely cause of this is the high osmotic value of the used media, viz. isotonic with the embryo environment in the ovule.

The nutrient for the postgerminal culture consisted of a salt solution with 0.8 % agar and 2 % sucrose. The embryos, grown to maturity, became transferred with big braking pipettes to the tubes, containing the nutrient. Figure 13 shows a number of young *Capsella* "seedlings": they were 200 μ when excised; the duration of the pregerminal culture in darkness was one week, after which postgerminal culture was started (photograph four weeks later); from this stage the young plants can be set out in earth. Figure 14 shows some plants, grown from cultured embryos, which accomplished their life-cycle in vitro.

Some interesting data about the germination of cultivated embryos were collected by P. van Oordt, B.Sc.. In a series of tubes, containing resp. 0 %, 3 %, 6 % and 12 % sucrose mature embryos were inoculated. No germination followed on the 12 % nutrient; on 3 % and 6 % sucrose growth after germination was about equal but on 0 % much less.

For a closer examination of the germinating embryos, they were laid out on moist filterpaper. Germination turned out to make its first appearance as an elongation of the cells near the basal end of the hypocotyl; next the rootlet developed and root-hairs grew out from the elongating cells. Soon this centre of elongation spread in both directions, causing participation of the entire hypocotyl after some time; in the mean time the cotyledons became green in colour. The cells of the hypocotyl elongated during this process from 20 μ to 120 μ. Figure 15 gives some drawings by P. van Oordt of germination stages. It was noticed that, coinciding with cell-elongation, for the first time tropistic phenomena came through.

In our opinion these data are noteworthy because they focuss the attention on the essential difference that exists between pre- and postgerminal growth; accordingly the conditions of cultivation in both stages ought to differ, as we postulated when starting this investigation. A further evidence for this view is offered by microscopical observation of immature embryos; excised torpedoes exhibit a precocious germination after transfer to a medium with an inadequately low osmotic value. This result forms a striking conformity with that of Ziebur and Brink (1951) on *Hordeum*.

DISCUSSION

1. There are two different criteria for judging in how far the embryo culture has succeeded. One of them lies in the success of

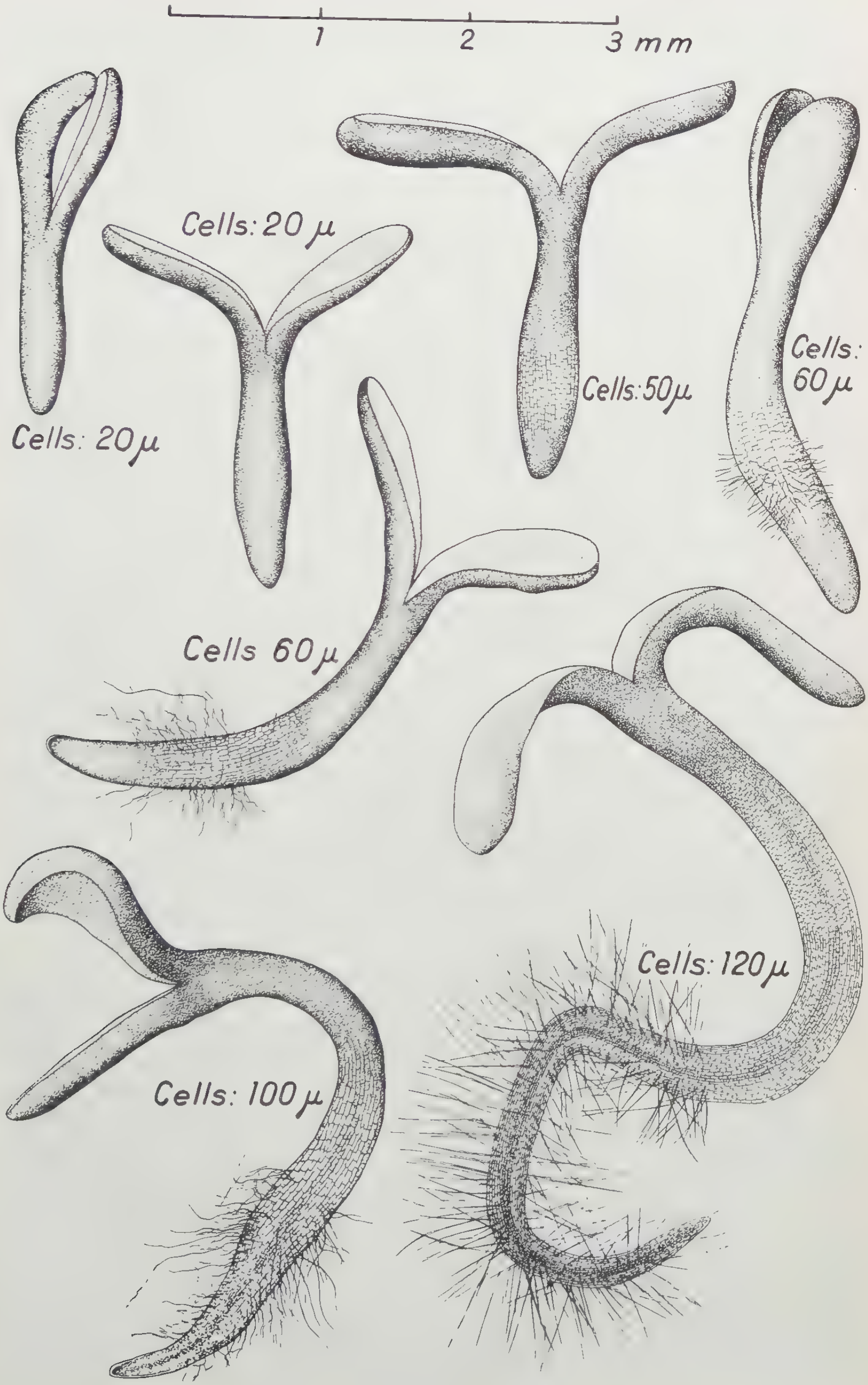

Fig. 15. Explanation see text.

attempts to cultivate embryos from a stage as young as possible to viable germs. The other criterion is how far one has succeeded in imitating *in vitro* the embryonic development in the ovule.

As to the first criterion we must state that embryos, smaller than abt. 100 μ, could not yet be cultivated; the globular stages never survived a transfer to *in vitro* conditions. The heart-shaped 100 μ stage proved to be very delicate: a large percentage of the inoculated embryos always died.

So we got stuck at about the moment the cotyledon-differentiation first appeared. At this point the original polyradiate symmetry becomes altered into a biradiate symmetry. This change may be accounted for by assuming an induction of it from gradients in the surroundings, that are biradial of nature. The cross-section of the ovule is elliptic, which offers some support for this hypothesis. The medium being homogeneous *in vitro*, here such gradients are naturally lacking.

In accordance with this we met an abnormal differentiation in some, though rare cases in young embryos, that developed a crown of more, e.g. 6, cotyledons at the apical end. In this respect earlier photographs of cultivated *Datura*-embryos are very illustrative (fig. 2—5, VAN OVERBEEK, CONKLIN and BLAKESLEE, 1942).

Yet the lack of gradients in the culture-medium cannot account entirely for the fact, that globular embryos could not be grown *in vitro*. Undoubtedly the composition of the medium itself was still deficient. The same holds to some degree for heart-shaped embryos, as is taught by a comparison of the growth *in vitro* with that *in ovulo*, in other words, by a judgement according to the second criterion.

Torpedo-shaped embryos, however, can stand such a comparison. In table VIII we find for these embryos a growth-rate of more than 80 % during the first day; this by no means lags behind the expectations, based on the growth *in ovulo*, as shown in figure 4. Conformity in metabolism may be concluded from the observation that fat accumulates *in vitro* as well as *in ovulo*. The presence of starch in both cases indicates that the interacting mechanism of fat-carbohydrate conversion is intact.

In table XX the data of a heart-shaped embryo, measured every 48 hours during 6 days, are compared with the expected growth: even in this favourable example growth lagged considerably behind that in the ovule. For such young embryos excision in itself certainly means a violent interference and the synthetic medium a change into new chemical and physico-chemical properties of the milieu. Another complication in imitating the embryo-milieu is, that quite probably changes occur during the development in the ovule, e.g. a decrease in the osmotic value. In the case of table XX the embryo was kept for 6 days in the same medium drop, containing 18 % sucrose, a concentration that is sure to be supra-optimal from the third day on, the embryo then having developed into a torpedo. A control experiment showed for embryos with an average initial length of 260 μ a mean growth of 42.5 % in 24 hours in media with 18 % sucrose whereas a mean of 63.5 % was reached in 12 % sucrose. So it is clear that the culture of small embryos possibly would be markedly improved by a repeated transfer to media that change gradually.

In our cultures embryos did not show any cell-elongation; they kept growing as embryos do. Our statement in chapter IV may substantiate that the osmotic value of the milieu takes a major part in determining the type of growth that occurs.

TABLE XX

The growth *in vitro* of a young heart-shaped embryo during 6 days compared with the expected growth *in ovulo*. Medium IV with glutamine as N-source and 18 % sucrose; pH 6.2; darkness; temp. 25° C.

	Time in hours			
	0	48	96	144
Length *in vitro* in µ. . . .	104	260	488	739
Procentual increase . .		150	88	52
Length *in ovulo* in µ . . .		490	950	1360
Procentual increase . . .		364	265	179
Difference µ		230	462	521
Difference %		214	177	127

2. Our statement that glutamine surpasses the complete mixture of amino acids, provided nitrogen aequivalence has been guarded, is seemingly at variance with the paper of Sanders and Burkholder (1948) on the need of amino acids of *Datura* embryos (cf. page 164). Unfortunately the authors did not test glutamine, so that we cannot certify the reality of this difference.

Our results suggest that some amino acids, e.g. tyrosine and glycine, as administered to the embryo in our culture medium, are not suitable for *Capsella* embryos. Surely several amino acids in the complete mixture depreciate its potential nutritional value. In our experiments glutamine as the only source of nitrogen gave the best results. Yet the possibility exists that, as compared to glutamine alone, a still better growth might be secured by adding some other amino acids to a medium as the main nitrogen-source. The deficiency of our knowledge about compounds containing NH_2-groups, that certainly have a function in plant-tissues, is obvious when considering the review by Steward and Thompson (1950): in paper chromatograms of alcohol-soluble plant substances still 20 unidentified spots occurred that were stained by ninhydrin.

According to our experience, however, we sustain that protein synthesis, even in the youngest cultivated embryos, can proceed unlimitedly from glutamine as the only nitrogen-source. In this connection it is rather amazing to state, that the homologous compound asparagine appears to be of little use: very low growth values resulted when using media containing asparagine as the sole source of nitrogen (cf. table XV).

Apparently glutamine is unchallenged in taking a key-position in the nitrogen-metabolism. The prevalence of one amide over the other is a well-known phenomenon with seedlings. Whether asparagine or glutamine plays the predominant role seems to vary with the species. *Lupinus* has become a textbook example, in which the etiolated seedlings accumulate asparagine. In *Pisum* this very amide could be found in the pods during ripening and quite likely figures in a similar way in protein synthesis too (after a review by Robinson,1929). Street (1949) mentions in a review glutamine as the prevailing amide in the seedlings of *Brassicaceae* (*Cruciferae*), which agrees with our observations on the pregerminal phase.

Why in seedlings either of the two amides predominates, is still an unsolved problem. Schwab (1936) raised the hypothesis that the presence of a specific amidase would discriminate in this respect; after this view the plants could be divided in two groups: asparaginase plants and glutaminase plants. Apart from this generalization, which has been criticized already by Street (1949), we move against this view our experience with *Capsella* embryos. The vivid starch formation, noticed with asparagine as a nitrogen-source, indicates a "short-circuit" with the carbohydrate metabolism, presumably via the Krebs-cycle. In this case an explanation of the prevalence of glutamine should rather contain a consideration of a specificity of the transamination systems that interact with the keto-acids of the Krebs-cycle.

3. As mentioned above the growth of young embryos, cultivated in a medium containing salts, sucrose and glutamine, lags behind the growth *in ovulo*. Yet no improvement could be acquired by the addition of growth factors, viz. a large number of bios factors and some purine-derivatives, all of them substances that are generally considered to be important factors in metabolism. So we agree with the negative results of Sanders (1950), who also tried a number of these factors on *Datura* embryos. In the experiments of Rappaport, Satina and Blakeslee (1950) nucleic acid even proved inhibitory.

These results seem to be at variance with the issue of the *Pisum* research, where a great number of the factors in question has been found to be growth-promoting in the postgerminal culture. The embryos, however, used in these experiments, were highly differentiated, decotylated germs; removing of the cotyledons may quite well eliminate an important nutritional system, thus causing a heterotrophy on bios factors.

In the pregerminal embryo culture the investigators met with a number of obstacles that were due to a deficiency of the medium. Attempting to surmount these difficulties, they took refuge in using natural substrata, such as coconut-milk. According to Steward and Thompson (1950) in this sap a "protein stimulating substance" should be present besides the nitrogen containing nutritional factors; this argument is based on the investigation of Caplin and Steward (1948) on the culture of carrot root phloëm, but the facts mentioned by these authors do not justify this hypothesis. Van Overbeek, Siu and Haagen Smit (1944) cannot persuade us either of the ergone character of their "embryo factor" in coconut-milk. The mere statement of a growth promoting activity in a dilution 1 : 19000 (5 mg/100 ml) is no sound argument, because it does not inform us on any optimal concentration. In reality their embryo factor could be an amino acid as well; we proved clearly that amino acids act favourably in a concentration of 20 mg/100 ml, even though we did not use glutamine in that experiment (cf. fig. 12).

At the "Cold Spring Harbor Symposion" (1942) VAN OVERBEEK suggested "auxin" to have an important regulatory function in embryonic development. SANDERS (1950) could not notice any influence of indole-3-acetic acid on embryo growth. Our experiments, however, yielded a real, though small influence. The results of a concentration series ranging from 0.001 to 10 p.p.m. show an effect somewhat similar to that on root growth, viz. stimulating in very low concentrations and inhibiting in higher ones. These effects, however, are far too small to implicate an important direct regulatory influence of hetero-auxin in embryogenesis.

SUMMARY

1. The distinction between pregerminal and postgerminal embryo culture has been defined and emphasized. The literature on the former has been surveyed from a physiological point of view.

2. Chapter II gives an account of the development of the embryo of *Capsella in ovulo*. The embryogenesis was divided in stages. The formula of the sigmoid growth curve could be determined by means of a graphical treatment of the data. Chemical and physico-chemical properties of the embryo and the endosperm were studied; the pH of the latter is 6.0 and the osmotic value is isotonic with 3/8 mol mannitol (8.4 atm). The osmotic value refers to ovules with "torpedoes."

3. Chapter III reports methods of and results with pregerminal embryo cultures.

a Culture cells were used for the cultivation of embryos, that were suspended in drops between two glasses so as to enable the observation of 25 embryos per vial. The growth was measured by a microscope with an ocular-micrometer.

b. In preliminary experiments on torpedoes (0.5 mm) the influence of some general conditions (pH, temperature and light) was examined.

c. Sucrose proved to be a superior source of carbon.

d. Casein-hydrolysate favoured the growth strongly.

e. A concentration series of a complete amino acid mixture verified that amino acids are limiting growth.

f. Ammonium lactate could not substitute amino acids as a food factor.

g. In cultures of heart-shaped embryos glutamine gave better growth than a nitrogen aequivalent, complete amino acid mixture. In

this respect glutamine proved to be exceptional and outstanding among the amino acids tried.

h. In contrast with glutamine, asparagine gave extremely low growth values, but in the embryos an abnormally rapid and strong starch production was observed.

i. Experiments on the influence of bios factors and purine derivatives gave negative results. Indole-3-acetic acid had a real, though small influence: it stimulated growth in a concentration of 0.001 p.p.m. and inhibited it in concentrations up from 1 p.p.m..

4. Chapter IV demonstrated the viability of cultivated embryos by means of postgerminal cultures. Germination appeared, when the osmotic value of the medium was lowered.

5. In the discussion the results of the cultures are confronted with the embryogenesis *in ovulo* and with the data of the literature.

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REFERENCES

BENSLEY, J. C., Hybridization of American 26 chromosome and Asiatic 13 chromosome species of Gossypium. Journ. Agr. Res. **60**, 175, (1940).

BLAKESLEE, A. F. and S. SATINA; New hybrids from incompatible crosses in Datura through culture of excised embryos on malt media. Science **99**, 331, (1944).

BONNER, J., Nicotinic acid and the growth of isolated pea embryo. Plant Physiol. **13**, 865, (1938).

Bonner, J. and G. AXTMAN, The growth of plant embryos in vitro. Preliminary experiments on the role of accessor substances. Proc. Nat. Acad. Sci. U.S.A. **23**, 453, (1937).

BONNER, J. and D. BONNER, Ascorbic acid and the growth of plant embryos. Proc. Nat. Acad. Sci. U.S.A. **24**, 70, (1938).

BRAUNSTEIN, A. E., Transamination and the integrative functions of the dicarboxylic acids in nitrogen metabolism. Adv. Prot. Chem. III, 1, (1947).

BRINK, R. A., C. D. COOPER and L. E. AUSHERMAN, A new hybrid between Hordeum jubatum and Secale cereale reared from an artificially cultivated embryo. Jour. Hered. **35**, 67, (1944).

CAPLIN, S. M. and F. C. STEWARD, Effect of coconut milk on the growth of explants from carrot root. Science **108**, 655, (1948).

CAPLIN, S. M., Nature **163**, 920, (1949).

COX, L. G., H. M. MUNGER and E. A. SMITH, A germination inhibitor in the seed coats of certain varieties of cabbage. Plant Physiol. **20**, 289, (1945).

CUMMINGS, J. M., Preliminary report on meiotic chromosomes in new Datura hybrids from embryos excised from incompatible crosses. Genetics, **30**, 3, (1945).

CURTIS, J. T., Undifferentiated growth of orchid embryos on media containing barbiturates. Science **105**, 128, (1947).

DICKSON, A. D. and B. A. BURKHART, Changes in the barley kernel during malting: chemical comparisons of germs and distal portions. Cereal Chem. **19**, 251, (1942).

DIETERICH, K., Über die Kultur von Embryonen auszerhalb des Samens. Flora **117**, 379, (1924).

Dormer, K. J. and H. E. Street, The carbohydrate nutrition of tomato roots. Ann. Bot. N. S. **13**, 199, (1949).

Doerpinghaus, S. L., Differences between species of Datura in utilization of five carbohydrates. Am. J. Bot. **34**, 583, (1947).

Duym, Chr. P. A., J. G. Komen, A. J. Ultee and B. M. v. d. Weide, The inhibition of germination, caused by extracts of seedballs of the sugar beet (Beta vulgaris). Proc. Kon. Ned. Ak. v. Wet. A'dam **50**, 527, (1947).

Fisher, R. A., Statistical methods for research workers. London, 1946.

Gautheret, G. J., Manuel technique de culture des tissus vegetaux. Paris, 1942.

Guignard, L., Recherches sur le developpement de la graine en particulière du tegument seminal. Journ. de Bot. **7**, 1, (1893).

Haagen Smit, A. J., R. Siu and G. Wilson, A method for the culturing of excised, immature corn embryos in vitro. Science **101**, 234, (1945).

Hannig, E., Zur Physiologie pflanzlicher Embryonen. I Über die Cultur von Cruciferen Embryonen auszerhalb des Embryosacks. Botan. Ztg. **62**, 45, (1904).

Hanstein, J., Die Entwicklung des Keimes der Monocotylen und Dicotylen. Hansteins Bot. Abh. **1**, 1, (1870).

Hausen, S. von, Effect of vitamin C (ascorbic acid) on the growth of plants. Nature **136**, 516, (1935).

Hausen, S. von, Bioch. Z. **288**, 387, (1936).

Jörgensen, C. A., The experimental formation of heteroploid plants in the genus Solanum. Jour. Genet. **19**, 133, (1928).

Kent, N. and R. A. Brink, Embryonic growth in vitro of immature Hordeum embryos. Am. J. Bot. **43**, 601, (1947).

Kögl, F. and A. J. Haagen Smit, Biotin und Aneurin als Phytohormone. Ztschr. Physiol. Chem. **243**, 209, (1936).

Laibach, F., Das Taubwerden von Bastardsamen und die künstliche Aufzucht früh absterbender Bastard-embryonen. Ztschr. f. Botanik. **17**, 417, (1925).

Laibach, F., Ectogenesis in plants. J. of Heredity **20**, 201, (1929).

Lammerts, W. E., Embryo culture an effective technique for shortening the breeding cycle of deciduous tree and increasing germination of hybrid seeds. Am. J. Bot. **29**, 166, (1942).

La Rue, C. D., The growth of plant embryos in culture. Bull. Torrey Bot. Club **63**, 365, (1936).

La Rue, C. D. and G. S. Avery, The development of the embryo of Zizania aquatica in the seed and in artificial culture. Bull. Torrey Bot. Club **65**, 11, (1938).

Le Heux, J. W. N., The growth curve. Proc. Kon. Ned. Ak. Wet. A'dam **50**, (1947).

Li, T. T., The development of the embryo of Ginkgo biloba. Sci. Rept. Nat. Tsing Hua Univ., Ser. B 2: 29, (1934).

Li, T. T. and T. Shen, The effect of "Pantothenic acid" on the growth of the radical of Ginkgo embryo in artificial media. Sci. Rept. Nat. Tsing Hua Univ. Ser. B 2: 53, (1934).

Lugg, J. W. H., Plant proteins. Adv. Prot. Chem. **5**, 230, (1949).

Mc Lean, S. W., New hybrids with the aberrant species, Datura ceratocaula, secured by embryo dissection. Genetics **30**, 14, (1945).

Merry, J., Studies on the embryo of Hordeum sativum. II The growth of the embryo in culture. Bull. Torrey Bot. Club **69**, 360, (1942).

Murneek, A. E. and R. O. Whyte, Vernalization and photoperiodism. 1948, Chron. Bot. Comp. Waltham Mass. U. S. A.

Olsen, C., The significance of concentration for the rate of ion-absorption by higher plants in water culture. C. r. lab. Carlsberg. Ser. Chim. **27**, 291, (1950).

Overbeek, J. van, Hormonal control of embryo and seedling. Cold Spring Harbor Symp. Quant. Biol. **10**, 126, (1942).

Overbeek, J. van, M. E. Conklin and A. F. Blakeslee, Cultivation in vitro of small Datura embryos. Am. J. Bot. **29**, 472, (1942).

Overbeek, J. van, R. Siu and A. J. Haagen Smit, Factors affecting the growth of Datura embryos in vitro. Am. J. Bot. **31**, 219, (1944).

Randolph, L. F., Embryo culture of Iris seed. Bull. Am. Iris Soc. **97**, 33, (1945).

Randolph, L. F. and L. G. Cox, Factors influencing the germination of Iris seed and the relation of inhibiting substances to embryo dormancy. Am. Soc. Hort. Sci., Proc. **43**, 284, (1943).

Robinson, M. E., The protein metabolism of the green plant. New Phytol. **28**, 117, (1929).

Rytz, W., Beitrag zum Aneurin stoffwechsel bei hoheren Pflanzen. Ber. Schw. Bot. Ges. **49**, 339, (1939).

Sanders, M., Embryo development in four Datura species following self and hybrid pollinations. Am. J. Bot. **35**, 525, (1948).

Sanders, M. E., Development of self and hybrid Datura embryos in artificial culture. Am. J. Bot. **37**, 6, (1950).

Sanders, M. E. and P. R. Burkholder, Influence of amino acids on growth of Datura embryos in culture. Proc. Nat. Acad. Sci. U.S.A. **34**, 516, (1948).

Sanders, M. E. and P. R. Burkholder, Effect of amino acids on growth of Datura embryos in culture. Am. J. Bot. **35**, 797, (1948).

Saubert v. Hausen, S., on the role of growth substances in higher plants. Physiologia Plantarum **1**, 85, (1948).

Schoorl, N., Organische analyse II. Amsterdam, 1937.

Schwab, G., Studien über Verbreitung und Bildung der Saüre-amide in der höheren Pflanze. Planta **25**, 579, (1936).

Skirm, G. W., Embryo culturing as an aid to plant breeding. Jour. Hered. **33**, 210, (1942).

Skorsted, A., Cytological studies in cotton. III A hybrid between Gossypium Davidsonii Kell. and G. Sturtii F. Muell.. Jour. Genet. **30**, 397, (1935).

Small, J., The hydrion concentration of plant tissues. I The method. Protoplasma **1**, 424, (1927).

Smith, P. G., Embryo culture of a tomato species hybrid. Proc. Am. Soc. Hort. Sci. **44**, 413, (1944).

Solomon, B., Inhibiting effects of autoclaved malt preventing the in vitro growth of Datura embryos. Am. J. Bot. **37**, 1, (1950).

Souéges, R., Les premières divisions de l'oeuf et l'origine de l'hypophyse chez le Capsella Bursa pastoris Moench. C. R. Paris **163**, 185, (1916).

Souéges, R., Les premières divisions de l'oeuf et les differenciations du suspenseur chez le Capsella Bursa pastoris Moench. Ann. sci. nat. **10**. Ser. Bot. 1, 1, (1919).

Spoerl, E., Amino acids as sources of nitrogen for orchid embryos. Am. J. Bot. **35**, 88, (1948).

Steward, F. C. and J. F. Thompson, The nitrogenous constituents of plants with special reference to chromatographic methods. Ann. Rev. Plant Physiol. **1**, 233, (1950).

Stone, E. C. and J. W. Duffield, Hybrids of sugar pine by embryo culture. J. For. **48**, 200, (1950).

Street, H. E., Nitrogen metabolism of higher plants. Adv. Enz. **9**, 391, (1949).

Tristram, G. R., Amino acid composition of purified proteins. Adv. Prot. Chem. **5**, 81, (1949).

Tukey, H. B., Artificial culture of sweet cherry embryos. Jour. Hered. **24**, 7, (1933).

Tukey, H. B., Artificial culture methods for isolated embryos of deciduous fruits. Am. Soc. Hort. Sci., Proc. **32**, 313, (1934).

Tukey, H. B., Growth patterns of plants developed from immature embryos in artificial culture. Bot. Gaz. **99**, 630, (1938).

Veldstra, H. and H. L. Booy, Researches on plant growth regulators. 17 Structure and activity. On the mechanism of the action. Biochim. et Biophys. Acta **3**, 278, (1949).

Werckmeister, P., Über die künstliche Aufzucht von Embryonen aus Iris Bastard samen. Gartenbauwiss. **8**, 607, (1934).

White, P. R., Plant tissue cultures. A preliminary report of results obtained in the culturing of certain plant meristems. Arch. Exp. Zellf. **12**, 602, (1932).

Zeuthen, E., A cartesian diver micro-respirometer with a gas volume of 0.1 μ l. C. r. lab. Carlsberg Ser. Chim. **24**, 479, (1943).

Ziebur, N. K., R. A. Brink, L. H. Graf, M. A. Stahmann, The effect of casein hydrolysate on the growth of immature Hordeum embryos. Am. J. Bot. **37**, 144, (1950).

Ziebur, N. K. and R. A. Brink, The stimulative effect of Hordeum endosperms on the growth of immature plant embryos in vitro. Am. J. Bot. **38**, 253, (1951).

RARE OR OTHERWISE INTERESTING MARINE ALGAE FROM THE NETHERLANDS

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Thanks to many collaborators, C. BRAKMAN, C. DEN HARTOG, Dr P. KORRINGA, J. A. W. LUCAS, A. MULDER, J. G. SLOFF, B. J. J. R. WALRECHT a.o. who sent Algae for identification to the Rijksherbarium and gave information about habitats, it is possible now to add new data to VAN GOOR's work on the Netherlands marine Algae. However, a complete review of the larger marine Algae occurring in that country can only be given after such genera as *Enteromorpha*, *Monostroma*, *Ceramium*, *Callithamnion* and *Ectocarpus* will have been revised for the Netherlands.

A *Rhodophycea* unknown from the Netherlands up to that time was collected by C. DEN HARTOG and A. MULDER in 1950. It was identified by the first collector. This Alga, **Dasya pedicellata** (Ag.) Ag. (syn. *D. elegans* (Mart.) Ag.), *Dasyaceae*, was collected in one of the canals in Zeeland, which contain seawater "Kanaal door Zuid-Beveland", Island of Zuid-Beveland. It was found growing in a great abundance in the same canal by several collectors in 1951. This locality is remarkable, for the species usually occurs in warmer regions: Mediterranean, Atlantic from southern Spain to Canaries (FELDMANN p. 94), Antilles (BØRGESEN p. 317), Atlantic coast of North America from Florida to Massachusetts (TAYLOR p. 355) and Pacific coast of Baja California (DAWSON p. 56). In Zuid-Beveland the species was found growing at a depth of 1—1½ m. TAYLOR records a depth of 1—4 m and FELDMANN dragged it from 25—30 m in the Mediterranean; FUNK (p. 456—457) also records this species at a great depth in the Mediterranean, though occasionally he found it at a depth of 10 m and even in one case near the water-mark.

Another *Rhodophycea*, unknown for the Netherlands up to this time, was collected by J. A. W. LUCAS (1950) in Schouwen, south coast near Zierikzee outside the dike, on the base of *Codium*, ± ½ m below low-tide mark. It was given to the author for identification and appeared to be **Phyllophora membranifolia** (Good et Woodw.) J. Ag., *Phyllophoraceae*. Its distribution is: Iceland, Norwegian west coast (Levring p. 110), Swedish west coast (KYLIN, 1944, p. 57), Danish coast (K. ROSENVINGE p. 521), British coasts (NEWTON p. 410), Atlantic coast of Belgium, France and Spain (Chalon p. 140) and of North America (Taylor p. 298).

A *Phaeophycea* previously unknown from the Netherlands, which came to the author's hands, appeared to be **Leathesia difformis** (L.) Aresch., *Leathesiaceae.* It was collected by K. Swennen (1950) on a shallow in the Balgzand (Wadden), east of Den Helder, growing on *Chaetomorpha linum.* Its gelatinous-fleshy, at first globose and solid, afterwards irregularly shaped, lobed and often hollow globules are ± 3—15 mm in diam. in the Netherlands specimens. A good picture of this species is to be seen in Kylin, 1947, fig. 46, T. 3 fig. 12. The distribution of this annual species is: Northern Ice-sea, Norwegian west coast (Levring p. 50), North Sea, Swedish west coast (Kylin p. 53), Baltic (Lakowitz p. 268), British coasts (Newton, p. 141), Atlantic coast of Belgium, France and Spain (Chalon p. 86) and of North America (Taylor p. 145), Japan, South Australia (A. H. S. Lucas, p. 102), New Zealand (Chapman, p. 63—68). *Leathesia difformis* is epiphytic on Algae and also on *Zostera* leaves, or grows on rocks; it is detached afterwards. It occurs in exposed places, at a depth of 0—1 m, in the littoral and higher part of the sublittoral zone.

Another *Phaeophycea*, up to this time unknown from the Netherlands is **Chaetopteris plumosa** (Lyngb.) Kütz., *Sphacelariaceae*, collected and identified by J. A. W. Lucas (1950). The Alga was abundantly growing on stones of the dike on the south coast of the Island of Schouwen, ± 1 m below low-water mark. Its distribution is: Northern Ice-sea, northern part of Atlantic (Taylor p. 133) and Pacific (Reinke p. 69), Norwegian coast (Levring p. 53), Swedish west coast (Kylin, 1947, p. 31), Baltic (Lakowitz p. 235), British coasts (Newton p. 193) and here and there along the Atlantic coast of France and northern Spain (Chalon p. 100). The Alga grows on stones and shells or is epiphytic; it occurs in the sublittoral zone.

In 1947 after an unusually hot summer, during which time no strong winds had been blowing, Dr P. Korringa collected a number of seaweeds in the oyster-basins constructed on the tidal flats near Yerseke, north coast of the Island of Zuid-Beveland, Oosterschelde, where, according to the collector, the salinity is 27 $^0/_{00}$. At low-tide the water in these basins still stands ± 1 m high. The collected seaweeds were sent to the author. Among them a number of species appeared to be rare in the Netherlands, while others were not collected before in this country. According to Dr Korringa, it is not possible to ascertain, whether or not these species have been transported on oysters, originating from abroad. It is true that between 1936 and 1940 fairly great numbers of oysters have been imported from France, the Gulf of Morbihan (Brittany) and from Arcachon, to the Oosterschelde. In 1944 again oysters have been imported from Brittany and in 1947 from Arcachon. The oysters there are not covered with water during some hours a day. The transport of these oysters packed in sacks lasts 4—5 days, sometimes in a rather high temperature. Though a few species of Algae might be imported from France, most of them surely are autochthonic. So far extends Dr KORRINGA's information.

An enumeration of the most interesting of the Algae from the oyster-basins follows here.

Fairly rare in the Netherlands is **Dictyota dichotoma** (Huds.) Lamour., *Dictyotaceae*. VAN GOOR (p. 68) records only one locality of this species, the Island of Tholen (on an oyster-shell). Among the Algae from the oyster-basins sent by Dr KORRINGA this species was represented; there was also a very narrow form (2 mm broad).

Dr KORRINGA informed the author that at one time this species had been fairly abundant in the oyster-basins, to the extent of being a nuisance then, but in 1947 it was rare. In 1950 and 1951 it was again very common there, and it has been collected in narrow as well as in broader forms. It was also found growing on the sea-dike near Wemeldinge, north coast of the Island of Zuid-Beveland (1951) and on the south coast of the Island of Schouwen (1950).

Later on a *Phaeophycea* was collected by C. DEN HARTOG (1950) in an oyster-basin at Yerseke, attached to a stone, and identified by the collector. It was a species unknown for the Netherlands up to that time, **Taonia atomaria** (Woodw.) J. Ag., *Dictyotaceae*. The species has the following distribution: British coasts (NEWTON p. 214), Atlantic coast of Belgium and France (CHALON p. 124), Mediterranean (HAUCK p. 308, FELDMANN, 1937, p. 179), Canaries (FELDMANN, 1937, p. 179).

Sphacelaria fusca (Huds.) Ag., *Sphacelariaceae*, was collected by Dr KORRINGA in 1937 in an oyster-basin near Bergen-op-Zoom. In 1951 it was collected by C. DEN HARTOG in an oyster-basin, Yerseke, at low-tide mark. It was also found growing on the south coast of the Island of Tholen on stones and on *Fucus serratus* (1951) and on the sea-dike of the Island of Texel, south of Oudeschild, on *Chaetomorpha* shortly above low-tide mark (1950). The thallus of the last mentioned specimen is only 7 mm long, whereas the Zeeland specimens are up to 3 cm long. *Sph. fusca* was kept separate from *Sph. cirrosa* (Roth) Ag. by HAMEL (1931—1939, p. 261), who followed in this SAUVAGEAU (1902, p. 393—399), on account of the shape of its propagules and the faint ramification. The species was not known for the Netherlands before. According to SAUVAGEAU (1902, p. 399) it occurs on the British coasts, the coast of Brittany and in Australia.

Gracilaria confervoides (L.) Grev., *Sphaerococcaceae*, recorded for the "Wadden", tidal flats, and the former Zuiderzee, near Medemblik, by VAN GOOR (p. 26), has been collected in the following islands: Schouwen, Zierikzee, mole (1939); Walcheren, "Arnemuidsch kanaal", at a depth of ½—1½ m (1941, 1942); Zuid-Beveland, harbour of Goes (1942), oyster-basins near Yerseke (1937, 1951), and "Kanaal door Zuid-Beveland" (1951). In 1884 A. A. WEBER—VAN BOSSE collected the species on the sea-dike of the Island of Texel, but it is not known, whether or not it was autochthonic there. The same holds for a specimen collected in the Oosterschelde by VAN DEN

Bosch (1842). *Gr. confervoides* usually occurs at low-tide mark, attached to stones and shells.

Hypoglossum woodwardii Kütz., *Delesseriaceae*, was also represented among the Algae from the oyster-basins, sent by Dr Korringa. Van Goor (p. 28) records the species for the Eendracht near the Island of Tholen growing on an oyster-shell, which was the only known autochthonic locality in the Netherlands then. A *Rhodophycea* sent to the author by B. J. J. R. Walrecht (1951) from Yerseke appeared to be this species too; it occurred at the base of *Codium* and on an oyster-shell. From the material sent to the Rijksherbarium for identification it appears that *Hypoglossum woodwardii* was likewise collected in other parts of the north coast of Zuid-Beveland, between Katse Veer and Sas van Goes on a stony slope in the lower part of the littoral zone (1948) and on the sea-dike near Wemeldinge (1951). It was also collected on the south coast of Schouwen (1941, 1950), where according to J. A. W. Lucas it was common in the lower part of the littoral and in the upper part of the sublittoral zone in 1950.

The species of *Polysiphonia, Rhodomelaceae,* collected in the oyster-basins have been treated by H. Veldkamp. After publication of his paper *P. violacea* (Roth.) Grev. and *P. nigra* (Huds.) Batt. were collected in an oyster-basin near Yerseke by J. A. W. Lucas and A. Mulder (1951). The first collector collected *P. nigra* also on Zeehondenplaat (Wadden), a shallow, east of the Island of Texel (1950).

Two species of *Chondria, Rhodomelaceae,* were among the Algae from the oyster-basins: **Ch. dasyphylla** (Woodw.) Ag. and **Ch. tenuissima** (Good. et Woodw.) Ag. Up to that time no localities of that genus were known for the Netherlands. Both species appeared to be still there in 1950, and also in 1951 they were collected again in the oyster-basins. *Ch. tenuissima* was found growing even luxuriously in 1951. *Ch. dasyphylla* has the following distribution: west coast of Sweden (rare, Kylin p. 88), Danish coast (K. Rosenvinge p. 406), British coasts (common, Newton p. 342), Atlantic coast of France (Chalon p. 164), Mediterranean, Antilles (Børgesen p. 259), Atlantic coast of North America from Florida to southern Massachusetts (Taylor p. 360); it is found growing on stones and shells below low-tide mark. Distribution of *Ch. tenuissima*: British coasts (Newton p. 342), Atlantic coast of France (Chalon p. 164), Mediterranean (Hauck p. 212), Atlantic coast of North America from Florida to Massachusetts (Taylor p. 359); it grows on stones and shells, shortly below low-tide mark and in the littoral zone.

Among the Algae from the oyster-basins at Yerseke there was also **Griffithsia devoniensis** Harv., *Ceramiaceae*, which is closely allied to *Gr. corallinoides* (L.) Batt. (syn. *Gr. corallina* (Lightf.) Ag.). Both species have the tetrasporangia arranged in the same way, i.e. in clusters surrounded by short incurved branches, situated near the common wall of two cells of a branch. Tetrasporangia are usually frequent and abundant in *Gr. corallinoides*, but rare and few in *Gr. devoniensis*. Rhizoids are always present up to the higher branches in *Gr. devoniensis*, they are less frequent and usually less numerous in *Gr. corallinoides*. The cells of *Gr. devoniensis* are cylindrical and slightly attenuate at the ends, they are about 130—335 μ wide and 4—9 × as long as broad. The higher cells of *Gr. corallinoides* are pyriform or ellipsoid, the ultimate ones are nearly globular; the higher cells (not the ultimate) are about 600—1100 μ wide and 2—4 × as long as broad. The upper part of the branches is moniliform. *Gr. devoniensis* was collected in 1841 by R. B. VAN DEN BOSCH in Zuid-Beveland, along the Zandkreek, drifted ashore. But the species was not recognized. It was described by KÜTZING under the name of *Callithamnion interruptum β setaceum* Kütz. and figured under the name of *Callithamnion setaceum* Kütz., Tab. Phyc. XI, 1861, p. 20 t. 63. Three specimens are preserved in the herbarium KÜTZING, which is incorporated in the Rijksherbarium, Leiden. The organ figured by KÜTZING as a cystocarpium (t. 63 fig. *c*) appeared to be a cluster of young tetrasporangia, after examination of the type. *Callithamnion interuptum β setaceum* Kütz. as well as *C. setaceum* Kütz. are thus synonyms of *Griffithsia devoniensis* Harv. KÜTZING described and depicted the last-named species in Tab. Phyc. XII, 1862, p. 9 t. 26, with tetrasporangia.

Gr. devoniensis is known in the Netherlands from Zeeland only. It was collected in the following islands: Schouwen, south coast near Zierikzee (1938, 1950); Walcheren, "Kanaal door Walcheren", not very rare (1940); Zuid-Beveland, Yerseke, oyster-basins (1947, 1950), "Kanaal door Zuid-Beveland" (1950, 1951) and Wemeldinge, seadike (1951). It was found growing in the littoral and sublittoral zones on stones. C. BRAKMAN stated that it prefers a shady place, but occasionally it occurs in a sunny place. In 1951 it was found growing in great abundance and bearing tetrasporangia.

Among the Netherlands specimens there are two from Schouwen (1938) and Zuid-Beveland (1950), in which the ultimate cells of the branches are nearly globular like in *Gr. corallinoides*. However, because of the possession of numerous rhizoids, the lack of pyriform cells and the slenderness of the cells, these specimens seem to belong to *Gr. devoniensis*. It is not impossible, that *Gr. devoniensis* is an ecological form of *Gr. corallinoides*. In favour of this idea are specimens bearing a fairly great number of tetrasporangia, but having long and thin cells.

Gr. devoniensis has the following distribution: southwest-point of England (NEWTON p. 368), Normandy and Brittany, Channel-Islands (Chalon p. 178).

Another species of *Griffithsia*, already known from the Netherlands before, **Gr. barbata** (Sm.) Ag. (VAN GOOR p. 38) was found again and recognized by C. DEN HARTOG (1950). VAN GOOR records the species for the Eendracht, whereas DEN HARTOG collected it in the oyster-basins near Yerseke.

A *Rhodophycea*, collected in the oyster-basins near Yerseke by several collectors in 1951, appeared to be **Antithamnion cruciatum** (Ag.) Naeg., *Ceramiaceae*. This species was known by VAN GOOR

(p. 42) from the "Wadden" and the northern part of the former Zuiderzee. It was also among the Algae collected by C. BRAKMAN in the Island of Walcheren, "Kanaal door Walcheren" (1940). In the Island of Zuid-Beveland it has been collected on a few more localities by several collectors: south coast near Ellewoutsdijk (1941), "Kanaal door Zuid-Beveland" (1951) and north coast near Wilhelminadorp (1951), thus along Westerschelde, Zandkreek and Oosterschelde. According to C. BRAKMAN the species occurs in shady places; it is always covered with water and is found attached to stones or posts between the stones of the dikes.

A *Chlorophycea*, among the Algae collected in the oyster-basins, **Bryopsis plumosa** (Huds.) Ag., *Bryopsidaceae*, was recorded by VAN GOOR (p. 131) only for Nieuwediep, the harbour of Den Helder, and Vlissingen, growing on posts. Later on the species appeared to be not so rare. It has been collected on the dike of the south coast of Texel (1950) and in Zeeland in the following islands: Schouwen, south coast, sea-dike (1949, 1950); Walcheren, "Kanaal door Walcheren" (1940, 1943); Zuid-Beveland, north of the Sloedam, abundant (1940), "Kanaal door Zuid-Beveland" (1951). It occurs at low-tide mark. C. BRAKMAN (1940—1943) found the species growing on sandstone and also on shells of *Mytilus* (living) in the soil of a creek, in places where the water remains, when tide is low, and slowly flows to and fro with the tide. The habitat may be shady or exposed to the sunlight.

A *Chlorophycea*, given to the author for identification by B. J. J. R. WALRECHT and collected by him at Yerseke (1950), outside an oyster-basin attached to a stone, shortly below low-tide mark, appeared to be **Cladophora arcta** (Dillw.) Kütz., *Cladophoraceae*, belonging to the section *Spongomorpha* Kütz., which is sometimes considered a separate genus. The species may be told by its broom-like, often semi-orbicular habit, its bright yellowish green colour, and its branches having long top-cells with dark green tips. A *Cladophora* very often collected by C. DEN HARTOG and J. A. W. LUCAS (1949—1951) in the harbour of Den Helder attached to wood, especially to rafts, was recognized by the author as to belong to the same species. The collectors saw the species only in the first months of the year, and after June it had disappeared everywhere. A. F. G. SLOOTWEG in his revision of the Netherlands Marine *Cladophora*'s mentions this species from Den Helder-Nieuwendiep only. For the first time it was collected in the Netherlands by A. A. WEBER—VAN BOSSE (1884), Durgerdam near Amsterdam, "het IJ", in that time brackish water.

Another *Cladophora* given to the author for identification appeared to be a species which was not included in the paper mentioned above. It is **Cladophora cristata** Kütz. found growing on the "Wadden", east of Texel (1950) and west of Terschelling (1951). Previously it was collected along the Zuiderzee by W. F. R. SURINGAR in 1854, near Hoorn and near Stavoren, on a sandy soil, in brackish water. This species is allied to *Cl. penicillata* Kütz., but differs in the characteristic habit: the more or less numerous main branches having distantly placed lateral branches 1—4 together, which are slightly branched at the lower part, but penicillate at the top; the ultimate ramifications are often pectinate. All cells are cylindrical. KÜTZING (1849, p. 404) based his description on *Conferva cristata marina* Roth. The director of the "Staatliches Museum für Naturkunde und Vorgeschichte", OLDENBURG, kindly gave the information, that the herbarium in 1926 was presented to the Botanical Museum, Berlin, where it has been destroyed during the war. Consequently the specimen from Norderney in herb. KÜTZING, preserved in the Rijksherbarium, Leiden, is the type-specimen now. The cells in this specimen are 120—130 μ in diam. and 4 × as long in the main branches, 50—65 μ in diam. and 1—5 × as long in the lateral branches, and 25—40 μ in diam. and 4—7 × as long in the ultimate branches; the top-cells are usually longer than the lower cells. In the Netherlands specimens the cells of the main branches are 140—270 μ in diam. and 3½—4 × as long, of the lateral branches 100—130 μ in diam. and 4—6 × as long, of the ultimate branches 30—100 μ in diam. and 4—10 × as long. HAUCK (p. 461) with a question-mark reduces this species to the synonymy of *Cl. glaucescens* (Griff.) Harv., of which the isotype, WYATT alg. Danm. n. 195, and a specimen in herb. KÜTZING which came from GRIFFITH have a different habit. *Cl. cristata* is very much alike certain forms of *Cl. glomerata* (L.) Kütz., a freshwater species. It may be a marine forma of that species. In herb. KÜTZING another specimen of *Cl. cristata* is present, which originates from the coast of Normandy.

Laminaria saccharina (L.) Lamour, *Laminariaceae*, was known to occur on stones of the sea-dike near Den Helder (VAN GOOR p. 71). It has been collected on the coast of Texel (1884, ? attached), Oudeschild, sea-dike (1950) and on the north coast of Zuid-Beveland, Kattendijke (1951). It was always found growing sublittoral.

Lithothamnion lenormandii (Aresch.) Fosl., *Corallinaceae*, was recorded for Den Helder (VAN GOOR p. 53). It has been collected on the north coast of Zuid-Beveland (1940, 1941, 1949, 1951), on the south coast of Schouwen (1950), and on the south coast of Tholen (1951). It occurs mostly on stones and sometimes on shells, at low-tide mark, often together with *Hildenbrandia prototypus* Nardo, *Ralfsia verrucosa* (Aresch.) J. Ag., a.o.

The marine **Bangia atropurpurea** (Roth) Ag. f. **fuscopurpurea** (Dillw.) Ag. (syn. *B. fuscopurpurea* (Dillw.) Lyngb.), *Bangiaceae*, was known by VAN GOOR (p. 15) from IJmuiden only. On reference to the collection of the Rijksherbarium this Alga can be recorded for the following localities now: Island of Texel, seadike (1950); Den Helder (1948, 1949, 1950); Callantsoog (1949); Hondsbosse zeewering (1950) [1]; IJmuiden (1893, 1950); Zandvoort (1946); Katwijk (1950); Noordwijk (1945); Hoek van Holland (1938, 1948, 1949); De Beer (1949); Island of Schouwen, south coast (1950); Island of Zuid-Beveland (1951), and near Cadzand, Zeeuwsch-Vlaanderen (1950) [1].

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[1] according to C. DEN HARTOG.

The substratum on which the marine *Bangia* occurs is mostly a wooden post or another wooden object, but also Algae and stones, usually in the upper part of the littoral zone, though in a few cases lower down, or in the spray zone.

HAMEL (1924, p. 446—447) saw no other difference between *B. atropurpurea* (Roth) Ag. and *B. fuscopurpurea* (Dillw.) Lyngb. than the environmental condition; yet he kept them separated, because *Bangia* was never found growing in water of low salinity in France. The same fact was stated for Denmark by KOLDERUP ROSENVINGE (p. 56), and KYLIN (1944, p. 10) had also the same opinion as HAMEL. However, LAKOWITZ (p. 297, p. 408), and M. WAERN (Exc. guide, Seventh Internat. Bot. Congr. Stockholm, 1950, 34) record *B. fuscopurpurea* for the Gulf of Bothnia, where the salinity is only 3—7 $^0/_{00}$.

In the Netherlands *Bangia* is likewise known from water of low salinity. It was collected in the former Zuiderzee, only near Kampen, where according to VAN GOOR (p. 10) the salinity was less than 10 $^0/_{00}$, on a stony slope (1855) and attached to a barrel (1931), the last mentioned locality according to HOCKE HOOGENBOOM (1936, p. 1). After the enclosure of the Zuiderzee in 1932, *Bangia* was collected in several places along the shores of what after that time is called "IJsselmeer", now an oligohaline lake (REDEKE, p. 21): Hindeloopen (1935), Lemmer (1935), Vollenhove, harbour (1932), Elburg, pier (1934), dike near Putten (1941), Den Oever (1950, 1951). According to A. VAN DER WERFF (Correspondentieblaadje Zuiderzee-Onderzoek VII, 1948, p. 5—9) *Bangia* occurred nearly everywhere on the dikes of the IJsselmeer in 1948. C. DEN HARTOG collected *Bangia* along the shore from Amsterdam to Hoorn in 1951.

The *Bangia* specimens collected in the Netherlands inland-waters up to now originate from Noord- and Zuid-Holland, and nearly all from waters called oligo- and mesohaline by REDEKE (p. 21). The first record, which is also mentioned in the Prodromus Fl. Bat. (p. 212) under the name of *B. atropurpurea* Ag., concerns abundant material growing on mosses along the river Merwede near Dordrecht (1843, 1844, 1856). Later on *Bangia* was collected in Leimuiden, Westeinderplas, on roots of Phanerogams (1941) and in Voorschoten, Vliet (1950). C. DEN HARTOG saw this species in several places in Noord-Holland (1951): Amstelmeer, Noord-Hollandsch Kanaal, Noordzeekanaal, Amsterdam (Amstel) and surroundings. It often occurs on stones at the water mark.

As *Bangia fuscopurpurea* (Dillw.) Lyngb. occurs in brackish water too, we may follow AGARDH (p. 76) and DE TONI (p. 3) in regarding the marine *Bangia* as a forma of the freshwater *Bangia*. In that case the name of the marine *Bangia* must be *B. atropurpurea* (Roth) Ag. f. *fuscopurpurea* (Dillw.) Ag. However, DILLWYN (T. 103) and afterwards AGARDH (p. 76) did not strictly separate the marine and the freshwater formae of *B. atropurpurea* (Roth) Ag., for in this species they combine specimens from marine localities as well as from mill-wheels. *B. atropurpurea* (Roth) Ag. was described from specimens growing upon mill-wheels in the vicinity of Bremen. It is true that the salinity of this locality is unknown, but it certainly tends to a freshwater locality rather than a marine one.

Though the freshwater *Bangia* may be regarded as reduced from the marine one (FRITSCH p. 397), the rule of priority does not allow to consider the freshwater *Bangia* as a forma of the marine one.

The freshwater *B. atropurpurea* (Roth) Ag. f. *atropurpurea* occurs in strongly moving water. PASCHER and SCHILLER (p. 159) mention mill-wheels, cataracts and weirs for the habitats of the freshwater *Bangia*. According to these authors it is mostly attached to wooden objects. C. DEN HARTOGH collected *B. atropurpurea* (Roth) Ag. in the "Loosdrechtsche plassen" (broads, 1951) on stones in a place, where waves were perceptable. It is the only strictly freshwater locality known in the Netherlands up to this time.

Though he does not use the feature for his key HAMEL notes that the freshwater *Bangia* has thinner filaments. PASCHER and SCHILLER (p. 159) record a diameter of the filaments of 13—60 μ for the freshwater *Bangia*, whereas HAMEL mentions for the marine *Bangia* a diameter of 20—150 μ and TAYLOR (p. 218) of 20—220 μ. FRITSCH (p. 426) records for *B. atropurpurea* as well as for *B. fuscopurpurea* an equal diameter up to 200 μ, but he mentions estuarine parts of rivers as the habitat of *B. atropurpurea*. In the Netherlands *Bangia* material the diameter of the filaments from the inland-waters is 24—78 μ, from the marine localities 40—130 μ, from the Zuiderzee collected before the enclosure 20—90 μ and after the enclosure (IJsselmeer) 25—65 μ.

Dumontia incrassata (Müll.) Lamour. (syn. *D. filiformis* (Fl. Dan.) Grev.), *Dumontiaceae*, was mentioned from the Netherlands by VAN GOOR (p. 52) only from Den Helder, where the species was collected several times up to now (Vangdam and sea-dike). The Rijksherbarium possesses specimens collected in 1852 along the north and northwest coast of Friesland. Further *D. incrassata* was collected near the Island of Terschelling and on its coast, narrow specimens, ½—1 mm broad (1938, 1948, 1949); on the coast of Vlieland (1950); on the southeast coast of Texel, thallus up to 7 mm broad (1949); on the south coast of Schouwen, in creeks (1947, 1950); along the Oosterschelde between Noord-and Zuid-Beveland, narrow thallus, less than ½—3 mm broad (1948); on the north coast of Zuid-Beveland (1951). It was found growing in the littoral zone, on dikes and shallows, often attached to stones, sometimes to shells. C. BRAKMAN saw the species in 1942 in great numbers in the Island of Walcheren, "Arnemuidsch Kanaal", to a depth of ± 1½ m; according to this collector the salinity is very low there, in winter down to 6 $^0/_{00}$. In the same year he saw the species in the harbour of Goes also in great numbers.

Cystoclonium purpureum (Huds.) Batt. (syn. *C. purpurascens* (Huds.) Kütz.), *Rhodophyllidaceae*, recorded for the Netherlands only from Den Helder (VAN GOOR p. 24), was collected moreover along the coast of Friesland, Barradeel, Dijkshoek (1852) and Harlingen (1904—1906), on the sea-dikes of the Islands of Texel (1887, 1950,

1951) and the Island of Schouwen, south coast (1939). The species was found growing attached to stones.

Rhodochorton rothii (Turt.) Naeg., *Ceramiaceae*, was recorded for the Netherlands from Den Helder (Van Goor p. 51), where it was collected again in 1948, 1949 and 1950 and from Delfzijl (1885), where it was collected again in 1950. This species has also been collected along the north coast of Friesland, Holwerd (1852), along the Zuiderzee, at that time brackish water (salinity ± 10 $^0/_{00}$, according to Van Goor p. 10), near Amsterdam (1884, 1885), on the sea-dike of Texel (1950) and it appears to be common in Zeeland, where it was collected in the following islands: Schouwen, south coast (1939, 1950); Tholen, south coast (1951); Noord-Beveland, south coast (1941); Walcheren, southeastern part and between Veere and Sloedam (1940), Sloedam, north side (1940); Zuid-Beveland, in many places along the coast (1940, 1941, 1950, 1951), and along the Oosterschelde (1845). The last-mentioned find was already recorded in the Prodr. Fl. Bat. (p. 178). *Rhodochorton rothii* is growing very often on posts, also on stones or clay between stones of dikes and breakwaters and on *Balanus*, in sheltered and shady places, from mean high- to mean low-tide mark; it has been collected in the *Fucus spiralis* zone as well as in the *Ascophyllum nodosum* zone.

Pelvetia canaliculata (L.) Decne et Thuret, *Fucaceae*, which, according to Van Goor (p. 67), occurred in one place in the harbour of Den Helder has disappeared since. Van Goor recorded this species also from IJmuiden, pier, and from Zeeland: Schouwen, Zandkreek and Oosterschelde. At present many more localities in Zeeland have been discovered: the coasts of Walcheren, Noord- and Zuid-Beveland along Oosterschelde, Westerschelde, Veersche gat, Zandkreek and Sloe. Moreover it was collected on the coast of Noord-Brabant, Steenbergen, de Heen. According to J. G. Sloff the species is wanting near Bergen-op-Zoom and the southern part of the Island of Tholen. According to C. Brakman (1940—1943) *Pelvetia canaliculata* often grows $\frac{1}{2}$—$\frac{1}{4}$ m below high-tide mark in Zeeland, above and sometimes in the *Fucus spiralis* zone; during spring tide it is sometimes immerged 1 m below the water mark; it occurs on the stones of the dikes and sea-walls, in rather shady places, exposed to the north or northwest. The *Pelvetia*-zone is sometimes short in Zeeland, but it can reach a height of 1 m. Other information from C. Brakman concerns the colour of *Pelvetia canaliculata* being dark brown to black in a dry state, but pale brownish yellow and swollen during rainy weather. *Pelvetia canaliculata* stands the frost in Zeeland.

C. Brakman (1940—1943) noticed on the north side of the Sloedam, between Walcheren and Zuid-Beveland the following zonation from top downwards. *Pelvetia canaliculata*, exposed, growing on the stones, among which species **Catenella repens** (Lightf.) Batt. (syn. *Catenella opuntia* (Good. et Woodw.) Grev.), *Rhodophyllidaceae*, in the holes between the stones, more or less sheltered. The zone of *Catenella*, however, is much longer than that of *Pelvetia* and continues lower down. Below this zone of *Pelvetia* and *Catenella* and partly mixed with it follows a zone of *Fucus spiralis* L. and lower down a zone of *Ascophyllum nodosum* (L.) Lejol. mixed with *Rhodochorton rothii.*

Near Rammekens (Ritthem), south coast of Walcheren along Sloe and Westerschelde C. BRAKMAN (1940—1943) saw the following zonation from top downwards: an *Enteromorpha* zone, a *Fucus spiralis* zone, an *Ascophyllum nodosum* zone and lower down *Fucus vesiculosus* L., *Fucus serratus* L., *Rhodochorton rothii*, *Hildenbrandia prototypus*, other *Rhodophyceae* and *Ralfsia verrucosa.* The zone of *Catenella repens* had its extension in the *Enteromorpha* zone to fairly high above that zone and lower down in the *Fucus spiralis* zone. In places where the *Ascophyllum nodosum* zone was less dense, *Catenella repens* was found growing to 1 m downwards in the *Ascophyllum nodosum* zone. In contradiction to *Rhodochorton rothii*, which can stand even the densest vegetation of *Ascophyllum nodosum*, *Catenella repens* disappears, when the *Ascophyllum nodosum* zone is too dense. On the other hand, C. BRAKMAN got the impression that *Catenella repens* avoids too much sunlight and prefers shady habitats. Three days continuous rain did no harm to *Catenella repens.*

This species was most often seen in the *Ascophyllum nodosum* zone and even lower down, but also many times in the *Fucus spiralis* zone and higher up in the *Pelvetia canaliculata* zone. It occurs on dikes, in cracks, in holes between the stones, filled with mud or sand, on wooden posts between the stones, on sandstone and bricks, but also on muddy saltings (schorren) in very shallow holes. In the last mentioned habitats the thallus is elongated and more or less filiform. VAN GOOR (p. 25) records this species from Oosterschelde and Westerschelde. Afterwards it has been collected in Schouwen, south coast (1941, 1948, 1950); Walcheren, south coast (1940, 1941); Sloedam, north and south side (1940); Zuid-Beveland, north coast (1941) and south coast (1940); Noord-Beveland, south coast (1941); thus along Westerschelde, Sloe, Veersche gat, Zandkreek and Oosterschelde. In no other province than Zeeland it has been collected up to now.

A *Rhodophycea*, which usually grows on muddy saltings is **Bostrychia scorpioides** (Gmel.) Mont., *Rhodomelaceae.* VAN GOOR (p. 36) only records this species for the Oosterschelde, as cited in the Prodr. Fl. Bat. (p. 171). He omits the locality on the shore of Friesland, also recorded in the Prodromus, since it is uncertain. Among the Algae sent by C. BRAKMAN from Zeeland (1940—1943) this species was not rare.

At present *Bostrychia scorpioides* has been collected in Zeeland: Schouwen, south coast, high up on the sea-dike (1950); Tholen, east coast (1949); Noord-Beveland, west coast (1931, 1949) and south coast (1940—1943); north of the Sloedam on the Walcheren side as well as on the Zuid-Beveland side, very numerous (1940—1943); Zuid-Beveland, southwest point, Kaloot (1940—1943), along Oosterschelde (1842) and Zandkreek (1840); in Noord-Brabant: Woensdrecht (1948, 1949). Thus *Bostrychia scorpioides* has been collected along Eendracht, Oosterschelde, Zandkreek, Veersche gat and Sloe. WEST-

HOFF (p. 227—228) saw the species in Terschelling, West, harbour. According to POST (p. 38) the distribution on this species is the following: Mediterranean, Atlantic coasts of Spain, France, Belgium, England, Scotland, Ireland and South, Central and North America up to Florida.

C. BRAKMAN (1940—1943) observed this species in the Zeeland habitats. He noticed that it grows on the basal part of Phanerogams on the muddy saltings, pressing its thallus closely against the stem and branches hard by the soil. Among the Phanerogams of the saltings *Bostrychia scorpioides* clearly prefers *Obione portulacoides* (L.) Moq. the base of which is densely covered by *Bostrychia*, when the *Obione* plants stand closely together. Where sheep are grazed, *Obione* disappears and so does *Bostrychia*. *Bostrychia* cannot stand an excess of sunlight. Where the habitat is too sunny, BRAKMAN found the colour

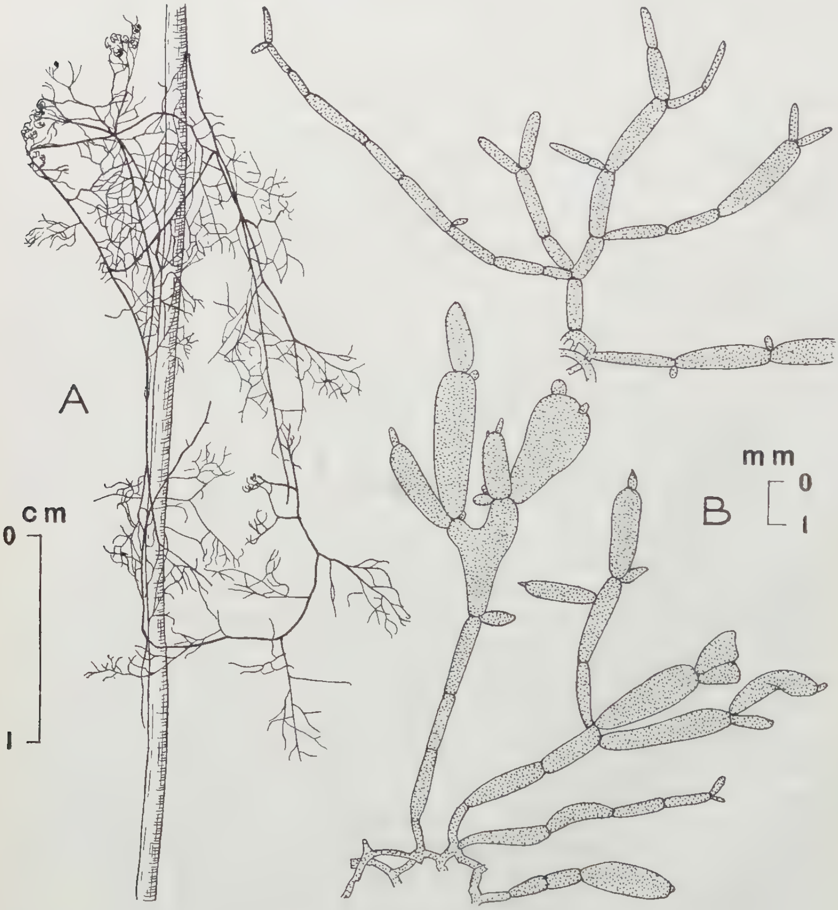

Fig. 1. A. *Bostrychia scorpioides* (Gmel.) Mont.; B. *Catenella repens* (Lightf.) Batt.

of *Bostrychia* bronze-green, in more shady places dark purplish red. Westhoff and Beeftink (p. 128) record that *Bostrychia* turns brownish green in very shady places and purplish to reddish brown in lighter habitats.

When not growing on *Obione* the *Bostrychia* plants often remain small. Other Phanerogams on which, according to C. Brakman, *Bostrychia* is found growing are *Spartina townsendii* H. et J. Groves, *Limonium vulgare* Mill., *Suaeda maritima* (L.) Dum., *Aster tripolium* L., *Puccinellia* and *Festuca*. Only once it was found growing on *Pelvetia canaliculata*. The species also occurs on the mud and, according to C. Brakman, sometimes on smooth stones. It can be found along the creeks, where the Phanerogams stand closely together and also in very shallow holes on the saltings. Sometimes *Bostrychia* is immersed only 2—3 hours a day. On the other hand, three days of incessant rain did no harm to *Bostrychia*. In spite of intense search of fructifications, none were found.

On muddy saltings there occurs also a remarkable *Phaeophycea*, **Fucus vesiculosus** L. var. **lutarius** Chauv. (syn. *Fucus lutarius* (Chauv.) Kütz.), *Fucaceae*. It has been collected along the Eendracht on the Noord-Brabant side (1939) as well as on the east coast of Tholen (1949, 1951), on the northeast coast of Duiveland, along the Grevelingen (1949), along the Oosterschelde (1841) and along the northern part of the Sloe in great quantities (1936, 1941, 1943). *F. vesiculosus* L. var. *lutarius* Chauv. was found along the Atlantic coast of Belgium, France (Hamel 1931—1939, p. 370; Davy de Virville et Dizerbo), Spain (Sauvageau p. 110—123), Portugal (Lami p. 178), and Morocco (Davy de Virville et Dizerbo, p. 33).

According to C. Brakman (1936) this *Fucus* forms a fine and crisp brown covering on the soil. It occurs in shallow holes as well as in creeks, sometimes where Phanerogams are wanting. The salinity of this habitat changes very much, owning to alternate desiccation and rains. The *Fucus* also penetrates into the mud or entwines the base of stems of Phanerogams. It grows among *Spartina stricta* and even higher, almost reaching freshwater. J. G. Sloff saw this *Fucus* also among *Triglochin maritima*. In some habitats the Alga is regularly immersed, in others this is not every day the case. C. Brakman saw the smallest specimens and the narrowest thallus in nearly always dry spots.

Chauvin (1831) discovered this alga in shallow pools in the mud, in the Island of Chausey. He considered it a variety of *Fucus vesiculosus*, but Kützing (1860) regarded it a separate species, in which he finally was followed by Sauvageau (1908), and Lami (1938—1939). However, the latter admits that in Portugal it is difficult to recognize this Alga as a separate species, because of its great variability. Sauvageau indicates the following features of the species: the creeping habit, the ribbon-shaped, often spirally twisted thallus, the numerous cryptostomata, the lack of vesicula and attaching disc and the mostly sterile condition. Lami saw the normal *Fucus vesiculosus* among *Fucus lutarius* without transitions and sometimes even attached on *Fucus* *lutarius*, otherwise growing in the mud. Moreover, he found a difference in colour between both Algae, being olive-brown in *Fucus vesiculosus* and more reddish brown in *F. lutarius*.

In some of the Netherlands specimens of *Fucus lutarius*, collected by J. G. Sloff, a few vesicula were present, as was also the case in specimens from the northern coast of Spain.

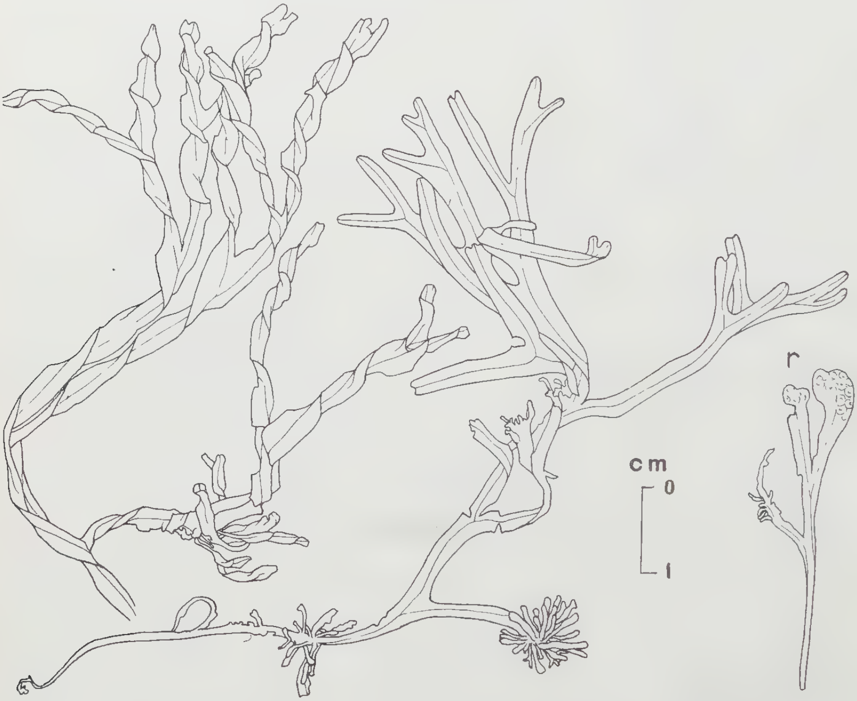

Fig. 2. *Fucus vesiculosus* L. var. *lutarius* Chauv.; r — receptacle.

Receptacula are rare indeed in *Fucus lutarius*. Sauvageau and Chemin saw only female receptacula, but Lami saw female as well as male receptacula. Among the material from Tholen collected by J. G. Sloff (1949) there was one specimen with a few poorly developed female receptacula. The present author prefers to follow Chauvin in considering *Fucus lutarius* as a variety of *Fucus vesiculosus*, because of the transitional forms having a few vesicula and the others bearing receptacula.

In the Prodr. Fl. Bat. (p. 180) this *Fucus* was described from specimens originating from the Oosterschelde, but it has been called *Fucus vesiculosus* L. f. *linearis* Ag., which is different from *Fucus lutarius*, according to Agardh (p. 276).

REFERENCES

Agardh, C. A., Systema Algarum, 1824.

Baker, S. M., On the brown seaweeds of the salt marsh, Norfolk — Journ. Linn. Soc. Bot, 40, 1912, p. 275—291; 43, 1916, p. 325—380.

Børgesen, F., The marine algae of the Danish West Indies II — Dansk Bot. Ark. 3, 1 e, 1919.

Chalon, J., Liste des Algues marines observées jusqu'à ce jour entre l'embouchure de l'Escaut et de la Corogne, 1905.

Chapman, V. J., The marine algal communities of Stanmore Bay, New Zealand — Pacific Science IV, 1950.

Chemin, E., Le Fucus vasicole de la baie de Terrénès — Rev. Algol. II, 1925, p. 146—157.

Dawson, E. Y., A further study of upwelling and associated vegetation along Pacific Baja California, Mexico — Sears Found. Journ. Mar. Res. X, 1, 1951, p. 39—58.

Dillwyn, L. W., British Confervae, 1809.

Davy de Virville et A. Dizerbo, Sur les Fucus vasicoles du Finistère — C.-R. somm. séances Soc. Biogéographie, 1943, p. 32—35.

Feldmann, J., Les algues marines de la côte des Albères — Rev. Algol. IX, 1937; Trav. Algol. I, 1942.

Funk, G., Algenvegetation des Golfs von Neapel — Pubbl. Staz. Zool. Napoli 7, Suppl., 1927.

Fritsch, F. E., The structure and reproduction of the Algae II, 1945.

Goor, A. C. J. van, Die Holländischen Meeresalgen — Verh. Kon. Ned. Akad. Wetensch. Amsterdam, sect. 2, deel 23, 2, 1923.

Hamel, G., Floridées de France II — Rev. Algol. I, 1924, p. 427—457.

Hamel, G., Phéophycées de France, 1931—1939.

Hauck, F., Meeresalgen Deutschl. und Oesterr., 1885.

Hocke Hoogenboom, K., Algae in Flora en Fauna der Zuiderzee. Suppl. 1936, p. 1—3.

Hocke Hoogenboom, K., Wierenbegroeiing van de IJsselmeerkusten 1932 tot (Juni) 1935 — Ned. Kruidk. Arch. 47, 1937, p. 280—330.

Kolderup Rosenvinge, L., The marine Algae of Denmark I, Rhodophyceae, 1909—1931.

Kuetzing, F. T., Species Algarum, 1849.

Kuetzing, F. T., Tabulae Phycologicae XI, 1861; XII, 1862.

Kylin, H., Die Rhodophyceen der Schwedischen Westküste — Lunds Univers. Årsskr. N. F. Avd. 2, 40, 1944.

Kylin, H., Die Phaeophyceen der Schwedischen Westküste — eod., 43, 1947.

Lakowitz, K., Algenflora der ges. Ostsee, 1929.

Lami, R., Sur quelques Fucacées de la côte de Portugal et leur repartition — Bol. Soc. Broteriana XIII, ser. 2, 1938—1939, p. 177—186.

Levring, T., Zur Kenntnis der Algenflora der Norwegischen Westküste-Lunds Univers. Årsskr. N. F. Avd. 33, 1937.

Lucas, A. H. S., The seaweeds of S. Australia, 1936.

Newton, L., British Seaweeds, 1931.

Pascher, A. und J. Schiller, Rhodophyta in Pascher, Süsswasserflora H. 11, 1925, 134—206.

Post, E., Systematische und Pflanzengeographische Notizen zur Bostrychia-Caloglossa-Assoziation — Rev. Algol. IX, 1936—1937, p. 1—84.

Prodromus Florae Batavae II, 2, 1853, p. 169—281.

Redeke, H. C., Hydrobiologie, 1948.

Reinke, J., Atlas deutscher Meeresalgen, 1889.

Sauvageau, C., Remarques sur les Sphacelariacées — Journ. de Bot. XVI, 1902, p. 393—416.

Sauvageau, C., Sur deux Fucus récoltés à Arcachon — Soc. Sci. d'Arcachon, Stat. biol. XI, 1908.

Slootweg, A. F. G., The Netherlands' marine Cladophora species — Blumea VI, 1948, p. 274—281.

Taylor, W. R., Marine Algae of the N. E. coast of N. America, 1937.

Toni, G. B. de, Intorno ad alcune Bangia di Bory e di Zanardini — Nuova Notarisia ser. XV, 1904.

Veldkamp, H., The genus Polysiphonia in the Netherlands — Blumea VI, 1950, p. 517—526.

Westhoff, V. en W. G. Beeftink, De vegetatie van duinen, slikken en schorren op de Kaloot en in het Noord-Sloe — Levende Natuur 50, 1950, p. 124— 13, 225—233.

THE AMYLOLYTIC ACTION OF MAPLE AND BIRCH SAPS

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INTRODUCTION

Canadian workers (1, 2, 3) have claimed the presence in maple sap of "sucrogène-amylase" and "cellobiogène-amylase" which transform starch into sucrose and cellobiose, respectively, and in birch sap, of a similar "cellobiogène-amylase" as well as a glucose-forming enzyme. In previous communications (5, 6), it was pointed out that these results could not be confirmed in Holland. In saps from 4 species of Dutch maple, only "ordinary" amylase, which converted starch to maltose and dextrin, was detected. Similarly, 5 species of birch possessed "ordinary" amylase and α-glucosidase (maltase) activity, but "cellobiogène" and "sucrogène-amylases" were absent. This and other evidence was apparently sufficient to render the Canadians' point of view untenable; the possibility remained, however, that minute quantities of cellobiose, more or less masked by the much larger amounts of sugar present in fresh saps, might have been overlooked. Attempts to eliminate the latter by dialysis through collodion membranes were not very successful.

The present report concerns further attempts to elucidate the phenomenon with the aid of filter paper chromatography and dialysis through cellulose membranes.

MATERIAL AND METHODS

A. *Saps*

The following species and hybrids were investigated: *Acer campestre* L., *A. cappadocicum* Gled., *A. dasycarpum* Ehrh., *A. Negundo* L. and *A. platanoides* L,; *Betula lenta* L., *B. papyrifera* Marsh and various *Betula* hybrids. In 1951 alone, 10 individual birch-trees were investigated, one of which was clearly a specimen of *Betula lenta*, while two of the others were identified as *Betula papyrifera*. The remaining seven were hybrids that were very difficult to identify.

The saps were collected as previously described (5, 6), care being taken to avoid contamination by bacteria, yeasts or saliva. Active enzyme preparations were prepared from the saps by precipitation with alcohol in the cold followed by rapid drying.

B. Dialysis

Fresh birch saps, as well as some concentrated by freezing, were dialyzed through cellulose membranes against (1) tap water, (2) neutral phosphate buffer and (3) a fluid obtained from concentrated saps by fermentation procedures (the latter, because co-enzymes might be functional in α-amylase action). There was little difference in activity among the various preparations, however, and the tedious fermentation method was soon discarded; dialysis against cold phosphate buffers was subsequently adapted as a routine method.

C. Filter paper chromatography

A mixture of *n*-butanol, acetic acid and water (160 : 40 : 200) was allowed to ascend during 20—24 hrs. in 20 by 40 cm pieces of Whatman No. 1 filter paper dotted with the unknown sugars; the sugar-spots were developed with the aid of *m*-phenylenediamine at a temperature of 110° C. This is essentially PARTRIDGE's procedure (7). It was found that distinction between maltose and cellobiose is very difficult by this method, the R_F-values being quite close together. For that reason, fermentation-methods were combined with filter paper chromatography, as will become apparent further on.

D. Quantitative sugar-determinations

The micro-fermentation method described by VAN LUTSENBURG MAAS and VAN ITERSON (4) was used throughout. One of the yeast-species applied fermented only hexoses, a second one hexoses plus sucrose, and a third one hexoses, sucrose and "maltose". It is probable that fermentable trisaccharides are included in the "maltose"-fraction.

E. Differentiation between α- and β-amylase

WIJSMAN's plate test (8, 9) was used but the results were difficult to interpret. Because of the relative heat-stability of the α-amylase expected to be present, concentrated saps were also kept at elevated temperatures (e.g. 65° C.) for extended periods; by means of this method definite conclusions as to the nature of the amylase could be arrived at.

EXPERIMENTAL RESULTS

A. Chromatography

The results are illustrated in figures I and II, idealized representations of the lower portions of developed filter-paper strips (actually, glucose and fructose spots partly overlap in the form of a figure-8). Only essential details are included; results from some control experiments with boiled enzyme, for example, have been omitted.

Birch saps. 6 of the 10 saps collected in 1951 contained only fructose and glucose (diagram I, No. 1), while 4 showed the presence of an additional sugar which, according to its position on the chromatograms, its vulnerability to invertase (diagram I, No. 3) and its fermentability (diagram I, No. 4) must be sucrose (diagram I, No. 2). It is worthy of note that 2 of the trees with sucrose in their saps were *papyriferas*. Cellobiose, which is nonfermentable, never appeared in the strips. Small quantities, however, when added to saps and sap-starch digests, survived the baker's yeast treatment and

Diagram I. For explanation, see text

	M *c*	*S*	*G*	*F*
1. Birch sap I			●	●
2. Birch sap II		●	●	●
3. Birch sap II after invertase action			●	●
4. Birch sap I or II after fermentation	·	·	·	·
5. Starch solution hydrolized by birch sap I.	●		●	●
6. Starch solution hydrolized by birch sap I, after invertase action	●		●	●
7. Starch solution hydrolized by birch sap I, then fermented	·	·	·	·
8. Starch solution hydrolized by birch sap I and fermented after addition of minute quantity of cellobiose	● *c*			
9. Starch solution hydrolized by birch sap I, then concentrated	●●		●	●
10. Birch sap I, concentrated			●	●
11. Maltose hydrolized by alcohol precipitate from birch sap I	●		●	
12. Starch solution hydrolized by alcohol precipitate from birch sap I	●		●	
13. Starch solution hydrolized by alcohol precipitate from birch sap I, then fermented	·	·	·	·
14. Starch solution hydrolized by alcohol precipitate from birch sap I and fermented after addition of minute quantity of cellobiose	● *c*			

were recovered as expected (diagram I, No. 8). Starch solutions, hydrolyzed by birch sap, always gave rise to a sugar which corresponded in position to maltose or cellobiose (diagram I, No. 5). Since it was inert to invertase action (diagram I, No. 6) and disappeared following the yeast treatment (diagram I, No. 7), thus excluding sucrose and cellobiose, respectively, it is most probably identifiable with maltose. In concentrated digests, yet another sugar was found, vulnerable to yeast and possessing a very low R_F value (diagram I, No. 9). The assumption that this sugar is a trisaccharide is very well compatible with the conclusion (arrived at in our earlier papers) that an α-amylase is active in the birch saps.

By the use of alcohol-precipitates from birch saps, it could be shown that both glucose and maltose are produced from starch (diagram I, No. 12). Whether the presence of these two sugars is due to the action of one single enzyme, an α-glucosidase with a great specificity-range, remains to be decided. The fact that the glucose-spots in chromatograms of starch/enzyme digests appeared stronger than those obtained from experiments with enzyme plus maltose (diagram I, No. 11) seems to favor the one enzyme concept.

Maple saps. These saps contained sucrose and amylase, but were devoid of hexose sugars and enzymes producing glucose from maltose or starch. For particulars, see diagram II.

Diagram II. For explanation, see text

	M c	S	G	F
1. Maple sap		●		
2. Maple sap after invertase action.			●	●
3. Maple sap after fermentation	·	·	·	·
4. Maple sap fermented after addition of minute amount of cellobiose	● c			
5. Starch solution hydrolized by maple sap.	●	●		
6. Starch solution hydrolized by maple sap, then fermented	·	·	·	·
7. Starch solution hydrolized by maple sap and fermented after addition of minute quantity of cellobiose	● c			
8. Starch solution hydrolized by alcohol precipitate from maple sap.	●			
9. Starch solution hydrolized by alcohol precipitate from maple sap, then fermented	·	·	·	·
10. Starch solution hydrolized by alcohol precipitate from maple sap and fermented after addition of minute quantity of cellobiose	● c			

B. *Quantitative sugar-determinations*

Some of the results have been summarized in table III:

TABLE III

Enzyme	Substrate, initial concentration in digest	Maltose (incl. fermentable trisaccharide) produced after 4 days at 35° C. and pH 6.0	Fermentable free hexose, produced after 4 days at 35° C. and pH 6.0
1. Birch sap, concentrated by freezing, then dialyzed against phosphate buffer pH 6.2 in the cold . . .	Starch 2.1 %	0.24 %	0.70 %
2. Birch sap, concentrated by freezing, heated at 65° C. for 20 min., and dialyzed against phosphate buffer pH 6.2 in the cold . . .	Starch 2.7 %	0.16 %	0.66 %
3. Same as 2, but unheated	Starch 2.7 %	0.32 %	0.55 %
4. Same as 3	Maltose hydrate 2.2 %		0.68 %
5. Alcohol precipitate from birch sap	Starch 2.7 %	0.35 %	0.70 %
6. Same as 5	Maltose hydrate 2.2 %		0.51 %

Since the iodine reaction in the starch digests had in all cases disappeared at the time of examination, while the amounts of sugars formed at that time were fairly small, the presence of an α-amylase relatively free from β-amylase must be assumed here. In concentrated birch saps it seems to possess a more marked insensitivity to heat than in fresh saps (table III, items 2 and 3; compare ref. 6).

To investigate the possibility that cellobiose might be present in the large fraction of the starch-enzyme digests not accounted for in the fermentation, one of the experiments carried out in 1947 with the aid of fresh maple sap was now repeated with dialyzed birch sap.

The sap was allowed to act on a starch solution till the iodine reaction had disappeared; then a little saliva was added and allowed to work. Under these conditions, 0.18 % of fermentable hexose and 2.25 % of "maltose" (incl. some trisaccharides) were produced from 2.5 % starch. Even though we have to make certain allowances for the relative inaccuracy of the micro-fermentation method, it is quite clear that, at the achroic point, only noncoloring dextrins can have been present besides the free sugars produced from the starch by the birch-enzymes: the unfermentable sugar, cellobiose, is not transformed into maltose by saliva. In other words: appreciable quantities of cellobiose simply cannot be present among the products of starch degradation.

DISCUSSION

In accordance with previous findings (5, 6), "ordinary" amylase activity yielding maltose from starch was demonstrated in both maple and birch sap. At the achroic point, the quantity of maltose is low, a fact which can be interpreted as evidence for an α-amylase. This would be in agreement with the relative thermostability noticed in birch amylase when present in concentrated saps.

When salivary amylase is allowed to act on a starch/tree sap digest after disappearance of the iodine reaction, the starch is converted almost quantitatively to fermentable sugars. From this it follows that there cannot be an appreciable amount of cellobiose among the initial products of starch degradation. The presence of cellobiose in tree saps and sap/starch digests, claimed by the Canadian workers BOIS et al. (1, 2, 3) could not be confirmed for Dutch trees. However, the possibility must be left open that birch trees yielding cellobiose in "commercial" quantities (1) are among the natural assets of Canada and not of Holland.

In starch/birch sap digests glucose was formed in addition to maltose. The question whether these two sugars are formed by different enzymes or by a single one, will be the subject of a separate paper.

SUMMARY

By means of filter paper chromatography and dialysis experiments combined with fermentation procedures, it was shown that maple sap contains an enzyme producing maltose but not cellobiose from starch. Birch sap contains an enzyme system converting starch into a mixture of maltose, glucose and dextrins, again without production of cellobiose. The amylases of maple and birch sap probably belong to the α-group.

It is a pleasure to thank the Elizabeth Thompson Science Fund for generous help in equipment.

REFERENCES

1. Bois, E. & W. O. Chubb, (1942). The sap of the birch tree, *Betula papyrifera* Marsh. I. The amylase system. *Canad. J. Res.* B, *20*, 114.
2. Bois, E. & A. Nadeau, (1938*a*). Contributions à l'étude d'*Acer saccharum.* II. La présence d'amylases dans la sève d'érable et les produits d'hydrolyse. *Canad. J. Res.* B, *16*, 114.
3. Bois, E. & A. Nadeau, (1938*b*). III. Action des amylases de la sève d'érable. *Canad. J. Res.* B, *16*, 121.
4. Lutsenburg Maas, H. J. van & G. van Iterson Jr., (1915). A micro-saccharimeter. *Proc. Kon. Akad. Wet. Amsterdam, 18*, 258.
5. Meeuse, B. J. D. (1943). Oriënterende onderzoekingen over de vorming van rietsuiker uit zetmeel in planten bij lage temperatuur. Diss. Delft.
6. Meeuse, B. J. D. (1949). Observations on the enzymatic action of maple and birch saps. *New Phytologist, 48*, 125.
7. Partridge, S. M. & R. G. Westall (1948). Filter-paper partition chromatography of sugars. I. General description and application to the qualitative analysis of sugars in apple juice, egg white, and fetal blood of sheep. *Biochem. J.* *42*, 238.
8. Wijsman, H. P. (1889*a*). De diastase, beschouwd als mengsel van maltase en dextrinase. Diss. Amsterdam.
9. Wijsman, H. P. (1889*b*). La diastase considérée comme un mélange de maltase et dextrinase. *Rec. Trav. Chim. Pays-Bas, 9*, 1.

A MONOGRAPH OF THE VOCHYSIACEAE
II. CALLISTHENE [1]

BY

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The genus *Callisthene* is found in the Extra Amazonian part of the Brazilian mainland, particularly in the zone of the campos and in the adjacent parts of Bolivia. The genus comprises eight species, as defined in this paper. It shows its greatest diversity on the central plateau of the Brazilian state of Minas Geraes. Most of the species are typical trees of the campos of the interior Brazilian plateau, which is characterized by a climate with a severe dry season.

The genus was first described by Martius in 1824. He mentioned all important characters and placed it in the *Vochysiaceae*, a family which had been described only four years earlier by A. de St. Hilaire (1820). It was named after *Callisthenes* (360—327 B.C.), the Greek naturalist and historian of Alexander the Great, relative and pupil of Aristotle. Martius (l.c.) described 3 species, Warming (1875 in the "Flora Brasiliensis") 7, while Briquet (1919) added several others, only one of which — in the opinion of the present author — can stand after careful studies of the complete type material.

Acknowledgments

The continuation of the investigation of the *Vochysiaceae* has been made possible by the courtesy and the coöperation of the following herbaria and institutions. These are indicated in this monograph by the abbreviations proposed in Part I of the Index Herbariorum by the International Association for Plant Taxonomy: The Arnold Arboretum (A), the British Museum of Natural History (BM), the Jardin Botanique at Brussels (BR), the Universitets Botaniske Museum at Copenhagen (C), the Chicago Natural History Museum (F), the Delessert and Boissier Herbaria in Geneva (G-DEL, G-BOIS), the University Herbarium of Goettingen (GOET), the Gray Herbarium (GH), the Instituto Agronomico do Norte (IAN), the Herbarium of the Royal Botanic Gardens, Kew (K), the State Herbarium at Leiden (L), the Jardin Botanico at Madrid (MA), the Missouri Botanical Garden (MO), the New York Botanical Garden (NY), the Oxford University Herbarium (OXF), the Muséum d'Histoire Naturelle, Phanérogamie at Paris (P), the Jardim Botanico of Rio

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[1] Part. I, comprising *Salvertia* and *Vochysia* in Rec. Trav. Bot. Néerl. Vol. XLI 1948, p. 397 seq., also in Med. Bot. Mus. Utr. 95 p. 397 seq.

de Janeiro (RB), the Naturhistoriska Riksmuseet at Stockholm (S), the Botanical Museum and Herbarium at Utrecht (U), the U.S. National Herbarium (US) and the Naturhistorisches Museum at Vienna (W), Botanische Staatssammlungen München (M).

The author wishes to express his sincerest thanks to the directors of these herbaria and institutes, the highly important collections having been put at his disposal in such a courteous and generous manner.

Morphological remarks

Callisthene is — like the other genera of the Vochysiaceae — very sharply defined and distinctly separated from the other genera by characters of important morphological value. These characters can be found in the structure of the flowers and the fruit. They will be discussed in some detail as they illustrate clearly the variations on the theme of the Vochysiaceous flower.

The *Vochysiaceae* can be divided in two tribes: the *Vochysieae* and the *Erismeae*[1]. The latter tribe, characterized by a unilocular, practically inferior ovary and an indehiscent fruit enclosed by the calyx-lobes, will be discussed in a subsequent section of this monograph.

The tribe of the *Vochysieae* comprises the genera *Salvertia*, *Vochysia*, *Qualea* and *Callisthene*. It is characterized by a trilocular superior ovary, by a free loculicidal capsule, which is not enveloped by enlarged calyx-lobes and by the simple or biramose hairs of the indumentum. The diagrams of the flowers of these genera are given in fig. 1.

It is apparent that *Salvertia*, with its five petals has — morphologically speaking — the simplest flowers.

The calyx is the most constant feature: no reductions or further specializations are found in this tribe. The fourth lobe is always larger than the others and practically always spurred. (The spur is absent in the subgenus *Amphilochia* of *Qualea*). In the *Erismeae* the calyx-lobes are enlarged after anthesis and envelop the fruit.

For the sake of convenience, the spurred lobe is often named the posterior lobe, the first and second lobes the laterals and the third and fifth ones the anterior lobes. This designation, often found in literature, is strictly speaking not accurate, as can be seen from the diagrams.

The corolla is extremely variable. A complete set of 5 petals, like the calyx quincuncially arranged and linking up with the aestivation of the latter, is to be found only in *Salvertia* (in the *Erismeae* in *Erismadelphus*). In the other genera the corolla is reduced. *Vochysia* has normally three petals, the aestivation of which does not completely agree with that of *Salvertia* (see part I p. 407). In a number of cases the lateral petals or even all petals are absent in *Vochysia*.

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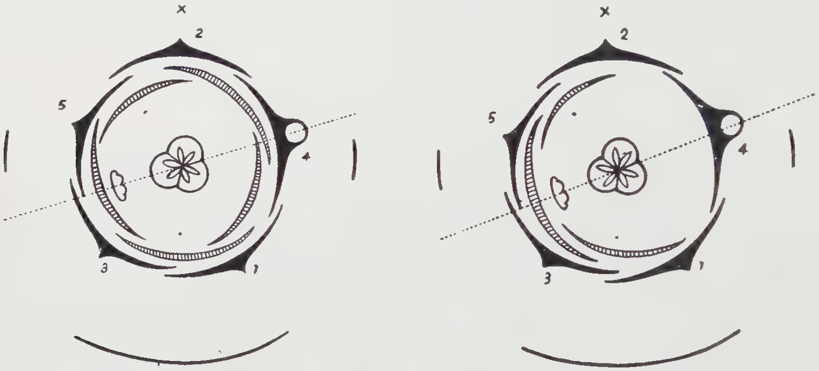
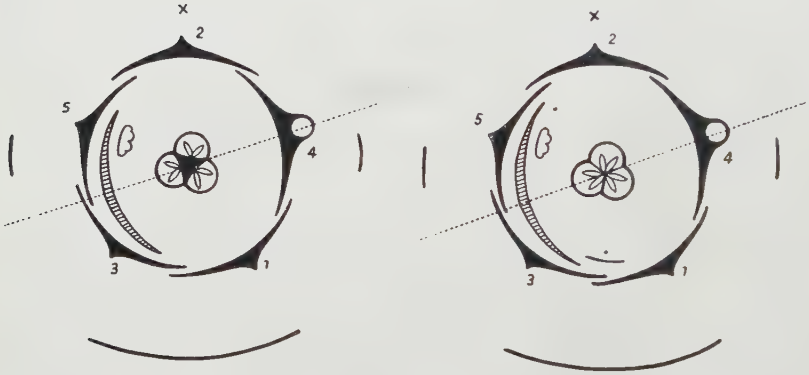
[1] *Vochysieae* Dumort. 1829 p. 6.
Erismeae Dumort. 1829 p. 6.

Qualea has one petal, like the central petal of *Vochysia* corresponding with the third petal of *Salvertia*. Rudimentary petals are sometimes met with in *Qualea;* they are found in the same places as the lateral petals of *Vochysia*.



Salvertia Vochysia



Callisthene Qualea

Fig. 1. Diagrams of the genera of the tribe *Vochysieae* Dumort.

Callisthene also has one petal, the third one. Rudimentary petals have not been found by the present author. This third petal, standing in the plane of symmetry of the flowers is apparently the most conservative element in the corolla.

The androecium too is varied. In each genus only one fertile stamen is found, not always, however, belonging to the same cycle. In *Salvertia*, *Vochysia* (and *Erismadelphus*) the fertile stamen stands in the symmetry plane at the base of the third petal (cf. diagram). 2 Staminodes belonging to this cycle are often found in each of these genera. In *Qualea*, *Callisthene* (and *Erisma*), however, the single fertile stamen stands in front of the fifth calyx-lobe, outside the plane of symmetry. The cycle to which this stamen belongs alternates with the corolla. The staminodes, however, are in the same situation as in *Salvertia* and *Vochysia:* alternating with the calyx. In *Callisthene* staminodes are mentioned by WARMING (1875 p. 21), but the present author has never seen any.

In the Vochysiaceous flower two cycles of stamens may be represented: it is only in the genus *Qualea* that both are present in the same flower.

The gynoecium is a very constant feature of the flower of this tribe, being always superior and trilocular. In each locule 2 ovules (*Salvertia* and *Vochysia*) or 2 series of ovules are found on the central placenta. The number of ovules per loculus in *Callisthene* may, however, be small or even one.

The fruit of the *Vochysieae* is a loculicidal trivalvous capsule. *Callisthene* differs since the exocarp, which is very fragile and more or less crusty, separates irregularly from the endocarp. The latter is regularly trivalvous (see fig. 3). These valves often split from the top along the midrib and then the fruit seems to be dehiscing with 6 equal valves. Another character in which the fruit of *Callisthene* differs considerably from that of the other genera is the presence of a thick and voluminous, persistent central column (see fig. 3 *c*, *d*).

The seeds of the *Vochysieae* are characterized by the presence of a wing. In *Salvertia*, *Vochysia* and *Qualea* the wing is unilateral and consists of numerous long hairs inserted on the testa. In *Callisthene*. the wing is a narrow and circumferential excrescence of the testa.

The stipules are completely obsolete or at most weakly developed in *Callisthene*. This reduction is generally not so extreme in the other genera. Those of *Vochysia* and *Salvertia* are small but distinct, the entire stipules being deciduous. This is not the case in *Qualea*. The stipules of this genus show remarkable specializations which will be discussed together with the taxonomic treatment of that genus in a subsequent part of this monograph. The absence or the extremely weak development of the stipules in *Callisthene* is in itself another further specialization of the genus, although diametrically opposed to that found in *Qualea*.

The vegetative buds of *Callisthene* are perulate, that is: furnished with a number of small brownish, protective scales. These scales, or cataphylls, are more or less persistent and are to be found at the base of the youngest branchlets (fig. 4e). The basal ones are crowded and the respective internodes are correspondingly short. In the section *Cataphyllantha* the most apical cataphylls bear the flowers.

Such perulate buds are mostly absent in *Vochysia* according to WARMING. The vegetative buds are naked and the younger branchlets bear no cataphylls at the base. On the contrary, the first internode is often longer than the subsequent ones and the first node bears normal frondose leaves. This feature is not so constant in *Vochysia* as Warming suggests. Several species have the same abbreviated internodes as *Callisthene*, in *Vochysia tucanorum* e.g. both structures can be found in different specimens. No semipermanent cataphylls are found at the bases of the branchlets: this agrees with Warming's observation that *Vochysia* is characterized by naked vegetative buds.

Perulate buds are also common in *Qualea*, although in many cases provided with only a small number of scales. In particular the species of the subgenus *Amphilochia* have the same structure as *Callisthene* and their first internodes too are extremely short.

The common feature of the inflorescence of all *Vochysiaceae* is the cincinnus. The cincinni may be arranged in numerous ways: in their simplest form they are one-flowered and stand in the axils of ordinary leaves. (*Callisthene* div. spec.). These one-flowered cincinni are recognizable as such by the presence of bracteoles on the pedicels. Strictly speaking, this denomination is wrong and the one-flowered cincinni are normal bibracteolate flowers. When comparing them with the normal 2-many flowered cincinni, often present even on the same branchlet, we feel justified in considering these axillary flowers as one-flowered cincinni. In other genera these cincinni may be arranged in racemes or panicles, the latter often constituting many-flowered thyrsoid inflorescences. The peduncles of the cincinni are well developed in *Salvertia* and *Vochysia* and in one or two species of *Qualea*. In nearly all species of the latter genus and in *Callisthene* the peduncles are reduced and the flowers are crowded in the axils of the respective bracts, cataphylls or ordinary leaves. The bracts and bracteoles are also crowded at the base of these e-pedunculate cincinni.

The supraspecific variation within the genus *Callisthene* is very slight. The main dividing issue is the position of the flowers on the branchlets. In the section *Callisthene* the flowers are placed in the axils of the ordinary (frondose) leaves; in the section *Cataphyllantha* they are placed in the axils of the cataphylls near the base of the branchlets. The leaves of the former section are generally small and the sterile branchlets with their numerous pairs of strictly distichously arranged small leaves have the aspect of a pinnately compound leaf; in some species the total branch system even resembles the leaves of *Caesalpinia*.

The flower is singularly constant in this genus: there is a slight variation in the shape of the small calyx-lobes but otherwise the variations are of minor importance. Further notes about the relationships are given in the taxonomic section in notes under the species.

Geobotanical and ecological remarks

The area of *Callisthene* is uniregional in Vester's sense (1940), being limited to South America. The species are found in two different phytogeographic zones (as defined by Sampaio 1934) e.g. in the zone of the *Campos* and in that of the *Caatingas*. Both zones belong to the Southern Brazilian (Extra Amazonian) Province of the Tropical American Territory (ENGLER 1912, SAMPIAO l.c.).

The eastern boundary of the area runs along the inner margin of the coastal rainforests. The southern boundary is less distinct, *C. hassleri* is the southernmost species, still found, however, in the campos. *Callisthene*, unlike *Salvertia* and *Qualea grandiflora*, does not feature in the savannas of Lower Amazonia. Generally speaking, the area corresponds to the zone of the Central Brazilian and Bolivian Campos, with a northern extension into the zone of the caatingas.

The Caatinga Zone is situated in N. E. Brazil and is characterized by tropical deciduous scrub forests. These scrub forests comprise a host of different types of vegetation, described by LÜTZELBURG (1923). *Callisthene*, like *Vochysia* and *Salvertia*, occurs in this zone in those places which can be considered as "disjunctions" of the Zone of the Campos (see part. I p. 411). The species are rarely found in the typical caatinga scrub forest.

The areas of the species are shown in fig. 2. Only two species are limited entirely to the Zone of the Caatingas. All the other

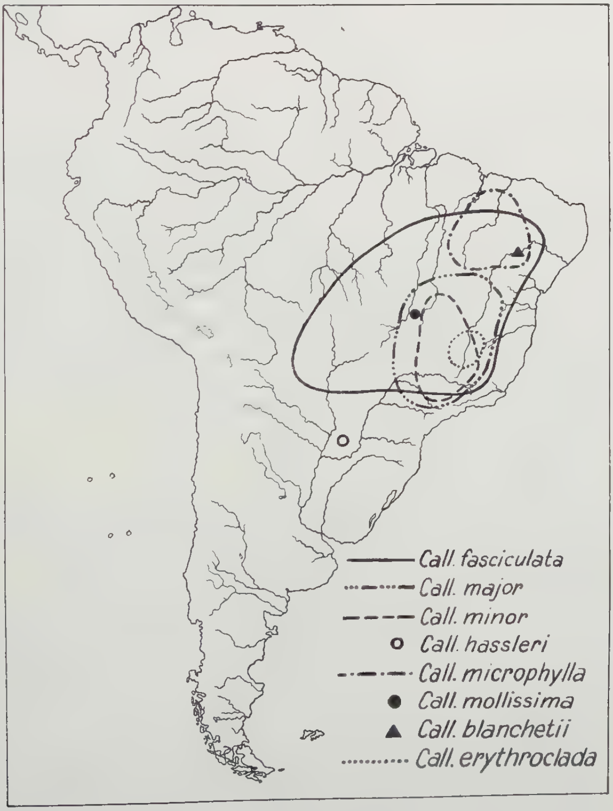


Fig. 2. Distribution of the species of *Callisthene* Mart.

species are found in the Zone of the Campos and constitute in it a very particular feature of the scenery.

The habitats of the species are listed in table I. All the species are trees from the campos cerrados (c.c.). These are parklike grass plains (savannahs) with scattered trees and small open forests. These thickets are locally called "capões". *C. fasciculata* seems to be found in the capões as well as in the open spaces. The other species — as far as can be ascertained from the scanty notes on the labels — seem to be found mostly in the capões.

TABLE I

Habitat and distribution of the species of Callisthene

	no. of coll.	Habitat	Phyto-geogr. Zone	Sect.
1. C. fasciculata	38	campos cerrados (c.c.) . . agreste and carrasco . .	Campos Caatingas	I
2. C. major var. major .	41	"capões" in c.c. . . . . campina and carrasco . .	Campos Caatingas	II
C. major var. pilosa .	9	"capões" in c.c.	Campos	II
3. C. minor	6	"capões" in c.c.	Campos	II
4. C. hassleri.	1	unknown	Campos	II
5. C. microphylla. . . .	9	campos, carrasco	Caatinga	II
6. C. mollissima	1	unknown	Campos	II
7. C. blanchetii	1	unknown	Caatinga	II
6. C. erythroclada . . .	3	"capões" in c.c.	Campos	II

c.c. means campos cerrados, see below.

C. fasciculata, *C. microphylla* and *C. major* are reported by Lützelburg (l.c.) in the zone of the Caatingas from typical campo vegetation ("campinas") as well as from "carrasco" (deciduous scrub forests with only a few *Cactaceae*) and from the "agreste", a formation with scattered, relatively tall, trees and a dense grass layer. *Callisthene* is never found in the typical caatinga formation, that is in the scrub forest characterized e.g. by numerous *Cactaceae*.

Notes and abbreviations

Most of the species of *Callisthene* are of very little economic value or even of no use at all. *C. fasciculata* is used as charcoal (Correa 1931 p. 109) and firewood. The name "Carvão branco" points also in that direction (lit. "white firewood"). The qualities as firewood are excellent on account of the presence of resins. The "variety" "Carvão vermelha" mentioned by Correa is not known from herbarium specimens.

The *abbreviations* which have been used for the herbaria are those given by Lanjouw in his lists in Chronica Botanica V p. 142—150 and VI p. 377—378. They are at the same time those proposed for the Index Herbariorum by the International Association for Plant Taxonomy.

Fl. Months during which flowering specimens have been collected.
Fr. Idem, fruiting specimens.
K^x Present in the Kew herbarium but not seen by the present author.

III. CALLISTHENE

Callisthene Mart., Nov. Gen. et Sp. I, 1824 p. 123; D. C. 1828 p. 25; A. Dietr. 1831 p. 95; Don 1832 p. 668; Meisner 1836—43 I p. 119, II p. 85; Endlicher 1836—40 p. 1177; D. Dietr. 1839 p. 20; Steudel 1841 p. 259; Benth. and Hook. 1862—67 I p. 976; Baill. 1874 p. 95; Warming 1875 p. 21; Petersen 1896 p. 317; Lemée 1929 I p. 762.

Trees or shrubs. Indumentum-if present-consisting of simple hairs. Branchlets opposite, distichous, the young ones at the base with several crowded cataphylls, the cortex sometimes more or less irregularly exfoliating, the fragments usually rather small; older branchlets glabrous, lenticellate. Perulate buds present. Stipules minute, sometimes subglandular, or obsolete. Leaves annual, simple, opposite, distichous, penninerved, equal-sided, often crowned with a brownish triangular gland, the margin entire. Flowers either solitary or in few-flowered — nearly e-pedunculate — cincinni in the axils of the cataphylls or the ordinary leaves, rather small — the bud 0.5—1.2 cm long — hermaphrodite, tetracyclic, irregular. Calyx gamosepalous, quincuncial, the base cup-shaped, the limb five-parted, the lobes unequal and deciduous, the fourth one spurred, as long as the flower-bud, çonvolute and enveloping the inner whorls, the other lobes smaller — the "lateral" ones often smallest. Corolla with the stamen perigynously inserted on the calyx; one petal, obcordate-obovate, the base cuneate-unguiculate, mainly yellow or yellow-white, membranous, glabrous, alternating with the third and fifth calyx-lobes, convolute, caducous. Stamen one, in front of the fifth calyx-lobe, glabrous, the filament cylindrical or subcylindrical, somewhat elongate after anthesis; the anther innate, oblong or sublanceolate, bithecate, the locules introrse, the connective produced beyond the locules but not cucullate; the pollen grains subglobose, tricolporate. Staminodes not present. Pistil tricarpellary, glabrous or nearly so. Ovary superior, ovoid, ellipsoid or subglobose, not sulcate, abruptly merging into the style, trilocular; the ovules epitropous, axile, few per loculus, inserted in two rows, the central placentas incrassate, integuments two. Style one, simple, cylindrical. Stigma terminal, capitate. Fruit a trilocular ellipsoid or subglobose capsule with one or few seeds per loculus, solitary on the incrassate pedicel. Exocarp fragile, crusty or somewhat woody, separating with irregular fragments from the endocarp, the latter regularly trivalvous loculicidal, the valves elliptic, pergamentaceous or somewhat woody, with prominent midrib inside, often split from the top along the midrib, brownish outside and yellowish inside. Central column persistent, thick, triangular with acute nearly winged angles. Seeds compressed, elliptic with rounded base and apex, the testa excurrent in a narrow circumferential wing, the hilum linear. Embryo straight, exalbuminous, the cotyledons plicate, the radicle very short and the plumule inconspicuous.

Distribution: Eight species in the dry regions of southern and central Brazil, northern Paraguay and eastern Bolivia.
Type species: Callisthene major Mart.
Ecology: Trees from campos, savannas etc.
Observation: The name has been derived from Callisthenes, the Greek historian and naturalist (360—327 B.C.).

Key to the sections

1*a*. Flowers in 2—3 flowered cincinni in the axils of the cataphylls, at most one or two in the axils of the lowermost ordinary leaves. Branchlets provided with 2—5 pairs of 3—17 cm long ordinary leaves. . . . . sect. A: **Cataphyllantha** p. 230.

b. Flowers solitary or rarely in 2-flowered cincinni in the axils of the ordinary leaves, at most one or two in the axils of the uppermost cataphylls. Branchlets provided with 5—15 pairs of 0.3—3 (rarely—5) cm long ordinary leaves . . . . sect. B: **Callisthene** p. 232.

section A. **CATAPHYLLANTHA** Stafl. nov. nom.

Warming 1875 p. 23 sub: "*Sect. I*". (gives latin diagnosis).

Flowering branchlets with three to nine pairs of opposite or subscattered, subconspicuous cataphylls and two to five pairs of opposite or subopposite foliage leaves; the latter medium-sized or large (3—17 cm long), not or only rarely provided with a triangular apical gland, not provided with a marginal nerve. Flowers in 2—3 flowered cincinni in the axils of the cataphylls or rarely in the axils of the lowermost foliage leaves. Flower-bud elongate-conical, acute-acuminate. Spur about as long as or somewhat shorter than the pedicel (0.6—1.0 cm). Anther about as long as or somewhat longer than the filament, the produced apical part subglandular.

Type species: Callisthene fasciculata Mart.
Distribution and Ecology: see under species.

1. **Callisthene fasciculata** Mart., Nov. Gen. et Sp. I, 1824, p. 126, II t. 100; Schult. 1827 p. 106; D.C. 1828 p. 26; A. Dietr. 1831 p. 96; St. Hilaire 1832 t. 192; Don 1832 p. 668; D. Dietr. 1839 p. 21; Warming 1875 p. 23, tab. 2; Spencer Moore 1895 p. 309; Malme 1905 p. 5, 6; Lützelburg 1923 III p. 225, 226; Correa 1931 p. 109. *Qualea fasciculata* Spreng. 1827 p. 10. *Callisthene floribunda* Gardner 1839 p. 333. *Qualea maliformis* Lk ex Warming 1875 p. 24. *Vochysia maliformis* Klotsch ex Warming 1875 p. 24. *Qualea excelsa* Glaziou 1905 p. 31 (nomen). *Qualea minaensis* Glaziou 1905 p. 31 (nomen).

Tree. Branchlets and leaves fulvous or brownish pubescent in varying degree, particularly along the nervation and the margin of the leaves, sometimes nearly glabrous. Petioles 0.2—0.6 cm long, Leaves on flowering branchlets membranous-subchartaceous, subdiaphanous, often 3—6 × 2—4 cm, the lower ones broadly obovate or suborbicular, with subobtuse or subrotundate, often emarginate apex and obtuse or rounded base, the upper ones elliptic or subovate with obtuse, rarely subacute or subrotundate apex and similar base. Older leaves subcoriaceous, shaped as the younger ones, up to 17 × 9 cm. Lateral nerves five to ten on each side, the bases often decurrent along the midrib, the angle with the midrib of the central ones about 50—60′, straight. Bracts and bracteoles linear, subulate, 0.2—0.3 cm long, together with the pedicels and the outside of the calyx pubescent or subpubescent. Pedicels slender, 0.7—1.0 cm long. Flower-bud 1.0—1.2 × 0.2—0.3 cm. Smaller calyx-lobes elongate-ovate, subsubulate, the laterals about 0.15 cm, the anteriors about 0.3—0.4 cm long. Spurred calyx-lobe elongate-ovate, acute-acuminate, 0.8—1.0 (— 1.2) × 0.5—0.6 (— 0.7) cm, the spur 0.6—1.0 cm long. Petal about $1\frac{1}{2}$—2 cm long and wide, apically rounded, yellow and — in particular in the centre — spotted with violet. Anther 0.6—0.8 cm long; filament 0.5—0.7 cm long. Ovary 0.2—0.3 cm long, the style 0.6—0.7 cm long. Capsule on the incrassate, obconical $\frac{1}{2}$—1 cm long pedicel, ellipsoid, 2—$2\frac{1}{2}$ cm long. Seeds about $1\frac{1}{2}$ cm long.

Type: Martius s.n. in Brazil, Minas Geraes between Serra de S. Antonio and Rio S. Francesco acc. to Martius (1824 p. 127). The type has not been seen by the present author: its whereabouts are not clear. In M. Martius' specimens from Piauhy and Bahia are preserved, but apparently none from Minas Geraes. The type sheet may have got lost temporarily or Martius' citation of locality may be erroneous. In the last case, the specimen from the Rio das Contas, Bahia in M ought to be chosen as the lectotype.

Type of *Qualea excelsa* Glaziou: Glaziou 20686 in P. Type of *C. floribunda* Gardner: prob. Gardner 1595 in BM. *Qualea minaensis* Glaziou is a name given to Glaziou 10740, 19151. The type(s) of *Qualea maliformis* Link ex Warm. and *Vochysia maliformis* Klotsch ex Warm. was (were) probably present in the Berlin herbarium. (Probably Sellow 2006).

Distribution: Southern and central Brazil and eastern Bolivia.

Brazil, Maranhão: Carolina, Krukoff 2056 (A, G-DEL, K^x, NY, U, US); — Pires and Black 2346 (IAN, U); —, — 2584 (IAN, U) Piauhy: Pussa, Lützelburg 1328 (M); Gardner 2569 (G-BOIS, G-DEL, GH, K, NY, P, US, W); Martius s.n. (M). Parahyba do Norte: Serra do Araripe, Lützelburg 12733 (F, M). Ceara: Grangeiro, Lützelburg 25992 (M), —, — 26167 (M); Gardner 1595 (G-BOIS, G-DEL, GH, K, L, NY, P, S, US). Matto Grosso: Cuyaba, Malme II 2545, 2545*a*; — , Riedel s.n. (OXF); Barra do R. d. Bugres, Lindman A 3179 (S); Spencer Moore 260 (K, NY, P), — 539 (K, NY), — 731 (BM, K); Gaudichaud 279 (P). Goyaz: Rio Taboca, Glaziou 20686 (BR, C, G-DEL, K^x, P); Natividade, Pohl 2327 (BR, F, W); Cavalcante-Conceiçao, Burchell 8105 (BR. GH, K, P); Sertao d'Amaroleitě, Weddell 2798 (P); Gardner 3141 (G-BOIS, G-DEL, K, NY, OXF, P, W). Bahia: Santa Rita, Zehntner (— v. Lützelburg) 3037 (M); Almas, v. Lützelburg 12740 (M, W); Martius s.n. (M); Minas Geraes: Corinto, Mexia 5586 (F, G-DEL, GH, K^x, MO, NY, S, U, US); Villa Funda, Glaziou 10740; Paracatú, Riedel s.n. (G. BOIS, GH, P, K, NY); Glaziou 19151 (C); St. Hilaire B$_1$ 1950 (NY, P); — s.n. (F, K, NY, P); Macedo 453 (MO); Claussen 55 (P); — s.n. (BM, K). Rio de Janeiro: Sao Fidelis, Glaziou 10741 (C, K^x, P). Locality unknown: Sellow 2006 (G.DEL, M, P, US); Claussen 163 (G-BOIS).

Bolivia, Sara, Santa Cruz, Buenavista, Steinbach 6592 (G-DEL, GOET, F, K, NY, S). Chiquitos: d'Orbigny 950 (BR, G-DEL, P); Weddell 3451 (P).

Ecology: Small tree of the campos cerrados. Flowers and leaves appear almost simultaneously shortly after the first rains. The leaves fall towards the end of the dry season (see Malme l.c.) In Bahia in "agreste" and "carrasco" (see p. 000.).
Vernacular Names: BRAZIL, Goyaz and Minas Geraes: Jacaré. Matto Grosso: Carvao Branco. Ceara: Cravo. BOLIVIA, Sara: Tinto Chico. (in lit.: Capitao do Campo sec. Correa l.c.
Use: Charcoal and firewood (Correa l.c.).
Observation: Carvao Branco means "white firewood". Pau de Terra means: "wood from the earth", a name given also to several other plants e.g. *Qualea* div. spec. Capitao do Campo ("captain of the field") is a name mostly given to *Cordia obscura* Cham. Cravo is a general name for many plants with Dianthus-like flowers.

section B. **CALLISTHENE**

Warming 1875 p. 23 sub: "*Sect. II*". (Gives Latin diagnosis).

Flowering branchlets with a small number of cataphylls and with six to fifteen pairs of opposite foliage leaves; the latter relatively small (0.3—3 cm long), distichous, — the branchlet often resembling a pinnate leaf, — nearly always provided with an acute triangular apical gland; a marginal nerve often present. Flowers solitary or sometimes in two-flowered cincinni in the axils of the ordinary leaves and sometimes a few in the axils of the uppermost cataphylls. Flower-bud conical, acute or subacute, spur short, about half as long as the pedicel or shorter. Anther shorter than the filament, the produced apical part short, not glandular.

Type species: Callisthene major Mart.
Distribution: Seven species distributed over the entire area of the genus.
Ecology: Trees from campos, savannas etc.

Key to the species

1*a*. Lower surface of the leaves glabrous 2
b. Lower surface of the leaves — at least of the young ones — pilose (sometimes mainly on the midrib) 5
2*a*. 8—15 pairs of leaves per branchlet, the leaves 0.3—0.9 cm wide 3
b. 5—7 (— 8) pairs of leaves per branchlet, the leaves generally wider than 0.9 cm. . . 2. **C. major** Mart. var. **major**
3*a*. Up to 11—15 pairs of leaves per branchlet 4
b. 7—9 (— 10) pairs of leaves per branchlet, leaves 1—2 cm long and 0.3—0.5 cm wide, oblong, elongate or lanceolate . . . . 3. **C. minor** Mart.
4*a*. Leaves 0.8—2.0 × 0.3—0.8 cm, strongly heteromorphous on each branchlet . . . . 4. **C. hassleri** Briq.
b. Leaves 0.3—0.6 × 0.2—0.4 cm, oblong or elliptic-oblong . . . . 5. **C. microphylla** Warm.
5*a*. Upper surface of the leaves glabrous or nearly so 6
b. Upper surface of the leaves densely tomentose . . . . 6. **C. mollissima** Warm.
6*a*. Indumentum on the lower side of the leaves spread over the entire surface or along the midrib only 7

b. Indumentum on the lower side of the leaves mainly along the nervation. Calyx-lobes subequal, shortly acute-acuminate . . . . 7. **C. blanchetii** Warm.

7*a*. 5—7 (— 8) pairs of leaves per branchlet. Calyx-lobes obtuse or acute. Indumentum on the branchlets fulvous or brownish . . . . 2. **C. major** Mart. var. **pilosa** Warm.

b. 10—15 pairs of leaves per branchlet. Indumentum on the branchlets ferrugineous. Calyx-lobes long acute-acuminate (if indumentum weakly developed and greyish see also n. 5, *C. microphylla* Warm.). . . . 8. **C. erythroclada** Warm.

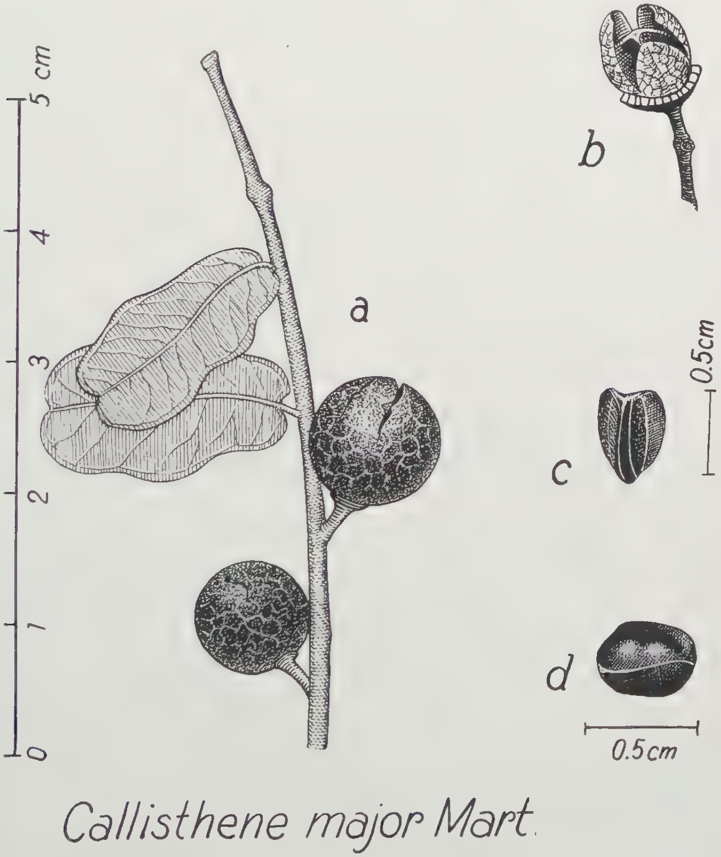


Fig. 3. *Callisthene major* Mart. *a*. Capsules; *b*. dehiscing capsule, the exocarp already separated from the endocarp; *c*. and *d*. central column of ripe fruit

2. **Callisthene major** Mart., Nov. Gen. et Sp. I, 1824 p. 124 fig. 75; Schult. 1827 p. 104; D.C. 1828 p. 25; A. Dietr. 1831 p. 95; Don 1832 p. 668 fig. 90; Warming 1875 p. 24 t. 3 fig. II; Malme 1900 p. 44; Lützelburg 1923 III p. 225, 226. *Callisthene durifolia* Briq.

1919 p. 378. *Callisthene clausseniana* Briq. 1919 p. 378. *Callisthene glazioui* Briq. 1919 p. 379. *Qualea disticha* Spreng. 1827 p. 10.

This publication fig. 3.

var. **major**

Tree. Branchlets and leaves glabrous or puberulous, the margins of the young leaves often ciliate. Flowering branchlets slender, about 0.1 cm wide and 8—12 cm long, with two to six — 0.2—0.3 cm long — cataphylls and 5—7 (— 8) pairs of ordinary leaves. Petioles 0.1—0.2 cm long. Leaf-blade variable in size, shape and texture according to age and position; on flowering branchlets subpapyraceous, subdiaphanous, mostly 2—3 × 1—1½ cm, the lower ones smaller, elliptic, oblong, obovate, or spathulate with a rounded emarginate apex, the upper ones elongate-elliptic or lanceolate, sometimes linear-lanceolate with acute apex; on fruit-bearing branchlets coriaceous, shaped as the younger ones, rarely up to 7 × 3 cm. Seven to fifteen subparallel lateral nerves on either side, the bases often decurrent along the midrib, the angle with the midrib about 30—60′, ending in the undulate marginal nerve. Pedicels 0.2—0.4 (— 0.5) cm long. Bracts and bracteoles ovate, up to 0.1 cm long. Flower-bud 0.8—1.0 cm long. Smaller calyx-lobes ovate or lanceolate, obtuse or acute, the laterals 0.3—0.5 cm, the anteriors 0.4—0.6 cm long. Spurred calyx-lobe elliptic-oblong, rounded, 0.8—1.2 × 0.5—0.6 cm; the spur 0.1—0.2 cm long, constricted near the base, often subglobose. Petal yellow, spotted with violet, about 1.1—1.4 × 1.2—1.5 cm, apically rounded, often subemarginate. Anther about 0.3 cm long, acute, the filament about twice as long. Ovary about 0.10—0.15 cm, the style 0.5—0.7 cm long. Capsule short-ellipsoid or subglobose, about 1½ cm long, the exocarp black with bluish pruina. Seeds about 0.7—1.0 × 0.4—0.6 cm.

Holotype: Martius s.n. in M from Tabaleiro, Vao de Parana. Type of *C. durifolia* Briq.: Claussen s.n. (1838—1839) in G-DEL.; of *C. clausseniana* Briq.: Claussen s.n. (1838—1839) in G-DEL; of *C. glazioui* Briq.: Glaziou 20681 in G-DEL.

Distribution: Central Brazilian Plateau.

Brazil, Minas Geraes: Numerous collections in many herbaria, e.g. Martius s.n. type (M); many collections of Claussen (e.g. the above-mentioned Briquet-types) and Warming. Goyaz: Natividade, Pohl 2315 (BR, F, M, U, US, W,); Pohl 2718 (BR, F, W); Pohl 1930 (BR); Capitao Vincente, Pohl 1744 (F, W); S. d. Pyreneos, Glaziou 20681, (BR, C, G-DEL, F, K, P); Tichoa, Glaziou s. n. (P); Burchell 6150 (BR, GH, K, P), — 6334—2 (K), —6411—2 (K), — 7650 (K). Bahia: Brejão, Froes 20096 (IAN); S. d. Tres Irmães, Lützelburg 527 (M, W); Sao Paulo: Bucido R., Lund s.n. (C). Loc. unknown: Schott 5 (W), — s.n. (K); Schuech s.n. (W).

Ecology: Often in the open bushes (capões) of the campos cerrados; in Bahia in Campinas and Carrasco (see p. 228). Fl. Aug.-Nov. Fr. Jan.-Apr.

Vernacular names: *Brazil,* Minas Geraes: Pao terra do mato (see obs. 4), Itapicury, Tiriba. Goyaz: Ja carié mirim.

Observation 1: This species is rather variable as regards the size and shape of the leaves, but the leaves are at least 1½ times (mostly 2—4 times) longer than those of the species 3—8.

— — — 2: The older leaves of this species are always coriaceous and sometimes also somewhat larger than those on the flowering branchlets. The latter are very young for the flowers and the leaves appear almost simultaneously. *C.*

durifolia Briq. and *C. clausseniana* Briq. have been described mainly on account of this difference in texture and some differences in leaf-size. It is clear that these species cannot be maintained. *C. glazioui* Briq. differs in no respects from *C. major*: the type specimen *Glaziou* 20681 has been compared by *Briquet* l.c. with *C. mollissima* and with *C. minor* but not with *C. major*, at least not with the Martius specimen. Between the latter and the former no fundamental differences are to be observed.

— — — 3: In describing this species together with *C. minor* and *C. fasciculata* Martius seems to have considered a capsule of *C. fasciculata* as that of *C. major*. See *Warming* l.c.

— — — 4: Pau terra is a name given to several species (*Callisthene*, *Qualea*). Mato means thicket.

var. **pilosa** Warm. in Flora Bras. XIII, II, 1875 p. 26. *Callisthene robusta* Briq. et Glaz. ex Briq. 1919 p. 379; Glaziou 1905 p. 30 nomen. *Callisthene mucronata* Briq. et Glaz. ex Briq. 1919 p. 381; Glaziou 1905 p. 30 nomen p.p.

Lower surface of the leaves, petioles, pedicels, and cortex of the young branchlets densely fulvous or brownish pubescent.

Holotype: Warming s.n. Lagoa Santa 6—9—1864 in C. Type of *C. mucronata* Briq. et Glaz.: Glaziou 20680 in G-DEL; type of *C. robusta* Briq. et Glaz.: Glaziou 20679 in G-DEL.

Distribution: Minas Geraes, Goyaz.

Brazil, Minas Geraes: Lagoa Santa, Warming s.n. 6—9—1864 (C); Corinto, Mexia 5597 (A, F, G-DEL, GH, K^x, MO, NY, P, S, U, US); —, — 5638 (A, F, G-DEL, GH, K^x, MO, NY, S, US); Arcos, Oliveira 224 (IAN), Lagoa Santa, — s.n. (IAN), Ant. Maihado do Sul, Schwacke 8922 (C). Goyaz: Sertao d'Amaroleité, Weddell 2762 (F, P); R. Descoberto, Glaziou 20680 (BR, C, F, G-DEL, K^x, P, S); Catalao, Riedel s.n. (G-BOIS, GH, K, NY); R. Paranaua, Glaziou 20679 (BR, C, G-DEL, K^x, P, S); Furnas—Pisarao, Burchell 5879 (K).

Ecology: see var. major.

Vernacular name: *Brazil*, Minas Geraes: Capucurú.

Observation: The specimen Glaziou 20769 (type of *C. robusta* Briq. et Glaz.) is bearing fruits and has the coriaceous leaves characteristic of this state. There are no further fundamental differences with the Warming type. The specimen Glaziou 20680 (type of *C. mucronata* Briq. et Glaz.) has rather smallish leaves but this variation falls easily inside a range of variability as for instance in the var. *major*.

3. **Callisthene minor** Mart., Nov. Gen. et Sp. I, 1824, p. 126 t. 76; Schult. 1827 p. 105; D.C. 1828 p. 26; A. Dietr. 1831 p. 95; Don 1832 p. 668; D. Dietr. 1839 p. 20; Schnizlein 1843—70 t. 260 fig. 3; Warming 1875 p. 27; Kuhlmann et Kühn 1947 p. 81. *Qualea minor* Spreng. 1827 p. 10.

Tree. Flower-bearing branchlets puberulous, subpuberulous or nearly glabrous, provided with seven to ten pairs of ordinary leaves, 5—8 cm long and up to 0.1 cm wide; the internodes distinctly shorter than the leaves. Older branchlets glabrous. Cataphylls about 0.1—0.2 cm long, two to six scattered and a few crowded near the base. Petioles about 0.1 cm long. Leaf-blade oblong, elongate-elliptic, lanceolate or linear, glabrous or nearly so, apex and base varying from acute to rounded, 1—2 × 0.3—0.5 cm, thinnish subpapyraceous in youth, coriaceous in age. Lateral nerves 6—10 on either side, irregular, ending in the undulate marginal nerve. Pedicels subpuberulous, about 0.2 cm long. Flower-bud 0.6—0.8 cm long. Smaller calyx-lobes unequal, ovate-elliptic, acute, ciliate and subpuberulous; the laterals about 0.2 cm long, the anteriors about 0.4 cm long. Spurred calyx-lobe broad-elliptic or ovate, about 0.8 cm long; the spur about 0.1 cm long, cylindrical. Petal yellowish, about 0.8—1.0 × 0.8—1.0 cm, apically rounded and often emarginate. Anther about 0.3 cm long, acute, the filament about 0.4—0.5 cm long. Ovary about 0.1 cm, the style about 0.5 cm long. Capsule ellipsoid, about 1 cm long.

Holotype: Martius s.n. in M, from Paranan.
Distribution: Mainly in Minas Geraes.
Brazil, Minas Geraes: Paranan, Martius s.n. (L, M); Ouro Fino, Regnell III 1539 (K, S, US); near Carmo, Regnell III, 1541 (K, S); S. Gonçalo, Widgren s.n. (S). Sao Paulo: Cabreuva, Hoehne 31011 (NY). Goyaz: Ule 201 (P).
Ecology: In open woods and bushes of the campos cerrados.
Vernacular names: Brazil, Sao Paulo: Itapiùna, Alecrim do Mato (the last name is often given to *Baccharis* species (Comp.) —).
Observation: Nearest related to *C. major* Mart. but differing from it by the size and the shape of the leaves. Differing from *C. blanchetii* Warm. by the glabrous leaves and the acute, not acuminate, smaller calyx-lobes.

4. **Callisthene hassleri** Briq. in Ann. Cons. Jard. Bot. Genève XX, 1919 p. 382.

This publication: fig. 4.

Flower-bearing branchlets slender, 10—15 cm long, minutely subpuberulous, provided with some cataphylls and 8—15 pairs of ordinary leaves, the internodes about as long as or slightly shorter than the leaves. Cataphylls 0—4 scattered and some crowded near the base. Petioles 0.1—0.2 cm long. Leaf-blades heteromorphous, glabrous except the ciliate margin, 0.8—2.0 × 0.3—0.8 cm, the central ones on each branchlet elliptic-oblong with rounded subemarginate apex and obtuse-subrotundate base, the basal ones smaller, shortly elliptic to suborbicular, the apical ones slender, lanceolate or lanceolate-elliptic with subacute, obtuse or subacuminate apex. Lateral nerves 6—10 on either side, ending in an undulate marginal nerve. Veins reticulate. Pedicels subpuberulous, 0.2—0.3 cm long. Bracts and bracteoles ovate, about 0.05 cm long. Flower-bud 0.8—1.0 cm long, slender. Smaller calyx-lobes unequal, ciliate and subpuberulous, the laterals elliptic or ovate, rounded or obtuse, about 0.2 cm long; the anteriors ovate or ovate-subelliptic, subacute, 0.4—0.5 cm long. Spurred lobe elliptic-oblong, 0.8—1.0 cm long, obtuse or subacute, the spur cylindrical, about 0.1 cm long. Petal about 1.0—1.2 cm long and wide, apically rounded or truncate, often emarginate. Anther about 0.3 cm long, acute; the filament 0.4—0.5 cm long. Ovary about 0.1 cm, the style about 0.4 cm long. Capsule unknown.

Holotype: Hassler 10638 in G-DEL.
Distribution: Once collected in N. Paraguay.
Paraguay, "In altaplanitie et declivibus Sierra de Amanbay", Rojas-Hassler 10638, (BM, F, G-BOIS, G-DEL, K^x, P, W).
Ecology: Fl. Sept.
Observation: Closely related to *C. major* Mart. and *C. minor* Mart. but differing by the long and slender branchlets with up to 15 pairs of leaves, the high

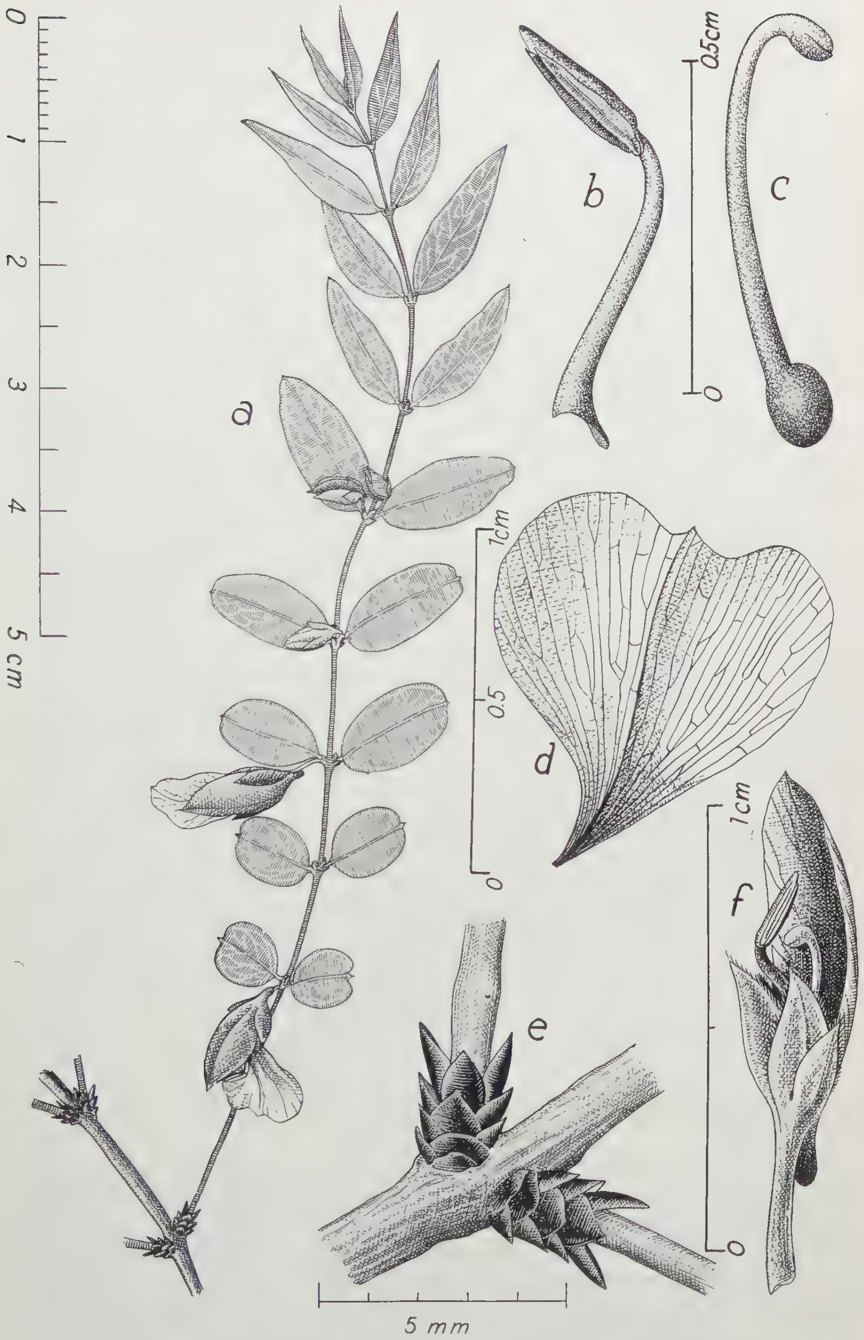


Fig. 4. *Callisthene hassleri* Briq. *a*. Young branchlet; *b*. stamen; *c*. pistil; *d*. petal; *e*. cataphylls; *f*. flower, the petal taken away

degree of heterophylly, the relatively large flowers and the elliptic, rounded or obtuse lateral calyx-lobes.

5. **Callisthene microphylla** Warm. in Flora Bras. XIII, II, 1875 p. 28 t. 3 fig. I.

Shrub or small tree, the branchlets and leaves whitish puberulous or glabrous. Ultimate branchlets about 3—7 cm long and up to 0.1 cm wide, provided with ten to fifteen pairs of ordinary leaves, the internodes about as long as or somewhat shorter than the leaves. Petioles up to 0.1 cm long. Leaf-blade oblong or elliptic-oblong, about 0.3—0.6 × 0.2—0.4 cm, the apex rounded or subtruncate, often emarginate, the base subtruncate or subcordate. Lateral nerves subconspicuous, four to five on either side; a proper marginal nerve absent; veins inconspicuous. Pedicels 0.1—0.3 cm long, provided with two ovate, subacute bracteoles. Flower-bud 0.4—0.5 cm long. Smaller calyx-lobes ovate, subacute, subpuberulous, the laterals about 0.15 cm, the anteriors about 0.2—0.3 cm long. Spurred calyx-lobe broadly ovate, obtuse, 0.4—0.6 cm long; the spur cylindrical, straight or subincurved, about as long as the pedicel. Petal about 0.5 × 0.5 cm, apically broadly rounded. Anther about 0.1 cm long, obtuse; the filament about 0.3 cm long. Style 0.3—0.5 cm long. Capsule ellipsoid-subglobose, up to 1.2 cm long, the base of the style subpersistent.

Holotype: Gardner 3142 in P. (see obs. 1).

Distribution: Bahia, Goyaz and Piauhy (Caatinga-region).

BRAZIL: Bahia: Chapada de Mt. Algre, Lützelburg 3027 (M). Piauhy: Gardner 2315, cotype (F, G-DEL, GH, K, NY, OXF, P, W); Serra do Brejo, Lützelburg 1747 (1746) (M, S (sub RB 16125), U (id.)); Urussuhy, Snethlage 625 (F); Martius s.n. (M). Goyaz: Gardner 3142, (F, G-BOIS, G-DEL, K, NY, OXF, P, W); Serra Geral, Lützelburg 630, also sub RB 5981 (M, S, U, W); —, — 1818 (M).

Ecology: In savannas, campos, carrasco etc. (see p. 228.).

Observation 1: WARMING l.c. mentions GARDNER 2315 first. This specimen bears fruits and in a note (l.c. p. 28) WARMING refers this specimen to GARDNER 3142, so that the latter may be regarded to be the type. In C. a drawing is found, made by WARMING after the specimen GARDNER 3142 from the herbarium de FRANCHEVILLE (now in P). It must be assumed that this has been WARMING's original specimen, moreover: the Paris specimen bears WARMING's handwriting.

Observation 2: This species differs from all other species by its very small leaves and flowers and by the relatively high number of internodes per branchlet. The branching systems with very young leaves have the appearance of leaves of *Caesalpinia* .

6. **Callisthene mollissima** Warm. in Flora Bras. XIII, II, 1875, p. 26.

Branchlets — except the older ones —, leaves, pedicels and bracts densely greyish-brownish or brownish tomentose. Ultimate branchlets 0.1—0.2 cm wide, provided with two to four cataphylls and six to nine pairs of ordinary leaves; the internodes mostly shorter than the leaves. Older branchlets with partly exfoliating cortex and immersed leaf-scars. Petioles about 0.1 cm long. Leafblade ovate-elliptic or suboblong-elliptic, 1—2 cm long and 0.5—1.2 cm wide, the apex rounded, truncate or — in young leaves — obtuse, the base rounded, the indumentum on the upper surface greyishglaucescent, on the lower surface brownish. Lateral nerves seven to ten on either side, anastomosing near the margin, the apical anastomoses constituting a marginal nerve. Pedicels 0.2—0.4 cm long. Bracts and bracteoles ovate, 0.1—0.3 cm long. Smaller calyx-lobes ciliate, pilose on the back, elliptic-ovate, acute, subacuminate or obtuse; the laterals 0.20—0.35 cm long, the anteriors 0.35—0.45 cm long. Spurred lobe broadly ovate, 0.7—0.9 cm long; the spur cylindrical, about half as long as the pedicel. Petal apically subtruncate. Anther about 0.3 cm long, acute, the filament about 0.4 cm long. Style about 0.6 cm long. Capsule unknown.

Holotype: Burchell 7871 in BR.
Distribution: Once collected in Goyaz.
Brazil, Goyaz: Between Goyaz and Cavalcante, Burchell 7871 (BR, GH, K, P).
Observation 1: The Brussels specimen bears *Warming's* handwriting.
— — — 2: Characterized by the indumentum, in particular by the tomentose upper surface of the leaves.

7. **Callisthene blanchetii** Warm. in Flora Bras. XIII, II, 1875 p. 26.

Tree of medium size. Flowering branchlets greyish-brown tomentose or pubescent, about 5—8 cm long, provided with a few cataphylls at the base and seven to eleven pairs of ordinary leaves; the internodes much shorter than the leaves. Adult branchlets glabrous, lenticellate. Leaves glabrous above and provided with long, crisp, undulating hairs along the nervation below; 0.7—1.5 × 0.4—0.8 cm; the basal ones obovate or oblong with rounded or truncate and often emarginate apex and rounded or obtuse base; the apical ones narrowly elliptic or lanceolate, with acute or subacute apex and acute or obtuse base. Five to eight lateral nerves on either side; marginal nerve present. Pedicels pubescent, 0.2—0.3 (— 0.4) cm long. Smaller calyx-lobes subequal, pubescent on the back, ovate-elliptic, shortly acute-acuminate or mucronate, 0.2—0.4 cm long. Spurred lobe broad-ovate, 0.6—0.8 cm long and up to 0.5 cm wide; the spur very short, equalling about one fourth of the pedicel. Anther about 0.1—0.2 cm long, obtuse; the filament about 0.4 cm long. Style about 0.5 cm long. Capsule unknown.

Holotype: Blanchet 2793 in BR.
Distribution: Once collected in Bahia.
Brazil, Bahia: Serra d'Açurua (Rio S. Francisco), Blanchet 2793, (BR, G-BOIS, G-DEL, F phot., K^x, MO, NY, OXF, P, W).
Ecology: "Dans les bois et les montagnes".
Observation 1: The Brussels specimen bears Warming's handwriting.
— — — 2: Characterized by the indumentum on the lower side of the leaves, the small size of the leaves, the extremely short spur, the obtuse anther and particularly by the ovate-elliptic smaller calyx-lobes, with a distinct acute-acuminate or even mucronate apex.

8. **Callisthene erythroclada** Warm. in Flora Bras. XIII, II 1875 p. 28.

Shrub or small tree, the leaf-bearing branchlets densely ferrugineous-tomentose, the lower surface of the young leaves subtomentose, the older leaves and branchlets glabrous. Branchlets 5—9 cm long, about 0.1 cm wide, with 10—15 pairs of ordinary leaves, at the base provided with some cataphylls; the internodes shorter than the leaves; older branchlets lenticellate. Petioles up to 0.1 cm long. Leaf-blade elliptic, broad-elliptic or oblong-elliptic, 0.8—1.2 (— 1.7) × 0.4—0.6 (—1.2) cm; the apex rounded or truncate, often emarginate; the base rounded or cordate. Five to seven lateral nerves on either side, irregular, the marginal anastomoses more or less constituting a marginal nerve. Pedicels 0.2—0.3 cm long. Bracts and bracteoles lanceolate, acuminate, up to 0.2 cm long. Smaller calyx-lobes subpuberulous on the back, subequal, the laterals lanceolate, about 0.3 cm long, long-acuminate, the top about 0.15 cm long; the anteriors ovate, acute, about 0.3—0.4 cm long. Spurred lobe broad-ovate, about 0.7 cm long, the spur about 0.1 cm long, cylindrical. Petal about 0.7 × 0.7 cm, apically broadly rounded. Anther about 0.2 cm long, acute, the filament about 0.3 cm long. Style 0.4—0.5 cm long. Capsule ellipsoid, up to 1.2 cm long.

Holotype: Pohl 3602 in W., leg. between Facenda Lopez and Sao Joao, Minas Geraes.

Distribution: Thrice collected in Minas Geraes.

Brazil, Minas Geraes: Between Facenda Lopez and Sao Joao, Pohl 3602 (F, W; in K sub 1958); Diamantina, Mello Barreto 9677 (F); Santa Luzia, Mello Barreto 8324 (F) (doubtful).

Ecology: In open bushes (capões) in the campos.

Observation: Characterized by the ferrugineous indumentum of the branchlets, the 10—15 pairs of leaves per branchlet and the long-acuminate lateral calyx-lobes and bracteoles.

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COLLECTOR'S NUMBERS

The numbers in parentheses refer to the running-numbers of the species of *Callisthene* used in this publication. The collector's numbers printed in *italics* are not mentioned in the text.

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Hoehne 31011 (3). Krukoff 2056 (1). Lindmann A. 3179 (1) Lutzelburg 527 (2); 630 (5); 1328 (1); 1747 (5); 1818 (5); 3027 (5); 3037 (1); 12733 (1); 12740 (1); 25992 (1); 26167 (1). Macedo 453 (1). Malme II 2545 (1); II 2545a (1). Mexia 5586 (1); 5597 (2); 5638 (2). Miers 2425 (2). Moore 260 (1); 539 (1); 731 (1). Oenike *44* (2). Oliveira 224 (2); *610* (2). Orbigny 950 (1). Pires & Black 2346 (1); 2584 (1). Pohl 1744 (2); 1930 (2); 2315 (2); 2327 (1); 2718 (2); 3602 (8). Regnell III 1539 (3); III 1541 (3). Schott *5* (2). Schwacke 8922 (2). Sellow 2006 (1). Snethlage 625 (5). Steinbach 6592 (1). Ule 201 (3). Weddell 2762 (2); 2798 (1); 3451 (1). Zehntner 3037 (1).

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REFERENCES

Baillon, H., 1874. Histoire des Plantes V 1874 p. 93.

Bentham and Hooker, 1862—67. Genera Plantarum I p. 975 seq.

Briquet, J., 1919. Decades Plantarum Novarum vel minus Cognitarum. Ann. Cons. Jard. Bot. Genève 20 1919 p. 342 seq.

CANDOLLE, A. P. DE (D.C.) 1828. Prodr. Syst. Nat. Reg. Veg. etc. Paris 1828 Vol. III p. 25 seq.

CORREA, M. P. 1931. Diccionario das Plantas Uteis do Brasil, Vol. II Rio de Janeiro 1931.

DIETRICH, A. 1831. Caroli a Linné Species Plantarum ed. Sexta. Vol. I.

DIETRICH, D. 1839. Synopsis Plantarum Vol. I 1839.

DON, GEORGE 1832. A general history of the dichlamydeous plants. London 4 Vls; Vol. II 1832 p. 668 (Vochysiaceae).

DUMORTIER B. C., 1829. Analyse des familles des plantes.

ENDLICHER 1836—40. Genera Plantarum. Wien 1836—40.

ENGLER, A. 1912. Syllabus der Pflanzenfamilien. 7 Aufl. 1912.

GARDNER 1839. Annals of Nat. Hist. III 1839 p. 333.

GLAZIOU A.F.M. 1905. Plantae Brasiliensis Centralis etc. in Bull. Soc. Bot. Fr. 52 1905 mém. 3.

HILAIRE, A. DE ST. 1820. Mémoire sur la nouvelle famille des Vochisiées in Mém. Mus. Hist. Nat. Par. VI p. 253.

HILAIRE, A. DE ST. 1832. Flora Brasiliae meridionalis Vol. III, Paris 1832—33.

KUHLMANN, M. et E. KÜHN, 1947. A flora do distrito de Ibiti, Sao Paulo 1947.

LANJOUW, J. 1939. On the standardization of herbarium abbreviations. Chron. Bot. V 1939 p. 142, VI p. 377—378.

LEMÉE, A. 1929. Dictionnaire descriptif etc. Vol. I p. 762.

LÜTZELBURG, PH. VON, 1923. Estudo Botanico do Nordéste. Rio de Janeiro 1923 Vol. III.

MALME, G. O. 1900. Ex Herbario Regnelliano III. Bihang till K. Svenska Vet. Akad. Handl. 25 afd. III no. 11 p. 44 seq.

MALME, G. O., 1905. Die Vochysiaceen Matto Grossos. Ark. Bot. V 1905 no. 6.

MARTIUS, C. F. P. VON et J. G. ZUCCARINI 1824. Nova Genera et Species Plantarum. München 1824 Vol. I.

MEISNER 1836—43. Plant. Vasc. Genera I p. 119.

MOORE, S. see Spencer le Marchant Moore.

PETERSEN, O. G., 1896. Vochysiaceae in Engler und Prantl's Pflanzenfamilien, Vol. III pars. 4 p. 312.

SAMPAIO, A. J. DE, 1934. Phytogeografia do Brasil. Sao Paulo 1934.

SCHNIZLEIN, 1843—70. Iconogr. fam. nat. etc. Vol. IV.

SCHULTES, J. A., 1827. Mantissa, Add. II ad Mant. I. Stuttg. 1827.

SPENCER LE MARCHANT MOORE 1895. The Phanerogamic Botany of the Matto Grosso Expedition 1891—92 in Trans. Linn. Soc. Bot. 2nd Ser. Vol. IV part. 3 1895.

SPRENGEL, C., 1827. Car. Linnaei Syst. Veg. ed. 16 Vol. IV Cur. Post.

STAFLEU, F. A., 1948. A Monograph of the Vochysiaceae. I. Salvertia and Vochysia, in: Rec. Trav. Bot. Néerl. XLI 1948 p. 397 and in: Meded. Bot. Mus. Utr. 95 p. 397 seq.

VESTER, H., 1940. Die Areale und Arealtypen der Angiospermen in: Bot. Arch. 41 1940 p. 1 seq.

WARMING, EUG., 1875. Vochysiaceae, in Flora Bras. vol. XIII pars II.

A NEW XYLOPIA FROM SURINAME (ANNONACEAE)

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Xylopia surinamensis R. E. Fr. n. sp. — Ramuli novelli dense aureo-ferrugineo-sericei, vetustiores plus minus glabrescentes et cortice densissime lenticellifero punctato vestiti; internodia 0,5—1 cm longa. Foliorum petiolus sericeo-tomentosus, 5—7 mm longus; lamina rigida, anguste lanceolata, basi rotundato-truncata, apicem versus sensim longeque attenuata, summo apice obtusa, supra ab initio glaberrima sed densissime verruculoso-punctata, subtus dense argenteo-sericea, 8—11 cm longa et 2—2,5 cm lata; costa supra valde impressa glaberrima, subtus prominens teres; nervi secundarii cum venulis vix conspicui. Flores in inflorescentiis densis nonnulli; bracteae numerosae, late ovatae, 1,5—2 mm longae. Sepala fere omnino coalita, calycem cupuliformem semiglobosum argenteo-sericeum 2—3 mm altum et 5—6 mm latum formantia. Petala exteriora linearia obtusa, extus argenteo-sericea, circ. 13 mm longa et 2 mm lata, prope basin subito dilatata; interiora linearia, acuta, quadrangulari-prismatica, utrinque cinereo-puberula, 12 mm longa et 1—1,2 mm crassa. Staminum filamenta 0,2 mm longa; antherae circ. 1 mm longae, locellatae, connectivi discus glaber; stamina exteriora plus minus sterilia. Pistilla numerosa (fere 30); ovaria dense sericea, circ. 1 mm longa, styli 1 mm et stigmata 1 mm longa. (Fructus ignotus).

Suriname: Boschreserve, Sectio O (florifera Junio 1944. — Wood Herbarium Surinam No. 139). Typus speciei in Herb. Utrecht).

It has not been possible to identify this type with any *Xylopia* hitherto known. The cup-shaped calyx with its highly connate sepals and the great number of carpels (up to 30) prove the affinity with *X. aromatica* and related species. The new species has smaller flowers and narrower leaves than *aromatica*, hairy branchlets in contrast to *nitida* and *longifolia* with their quite glabrous internodes. Very characteristic are the small, dense warts on the upper surface of the leaves, and also the abundant lenticels on the woody branchlets.

NOVITATES BURSERACEARUM II

BY

J. J. SWART (Utrecht)

(*Received December 15th 1951*)

Protium Bangii Swart n. sp. Arbor. Ramuli satis robusti teretes striati fuscescentes lenticellis ellipticis sparsis. Folia 2-juga circ. 15 cm longa ubique glabra juvenilia pilis nonnullis munita, petiolis semiteretibus basi subincrassatis 3,5 cm longis, interjugis teretibus supra carinatis 2 cm longis, petiolulis foliolorum lateralium semiteretibus subalatis 2—3 mm longis sed terminalibus teretibus carinatis 15 mm longis, foliolis elliptico-oblongis subovatis apicem versus valde angustatis 8 cm longis 3,75 cm latis lateralibus leviter asymmetricis basalibus in super brevioribus, omnibus apicem versus gradatim acuminatis, acumine attenuato 7,5 mm longo 5 mm lato, basi late cuneata vel rotundata, margine integro, pergamentaceis laevibus, nervis secundariis utrinque circ. 12 apicem versus prope marginem conjunctis, nervis primariis supra sulcatis infra cum sec. et tert. prominentibus. Inflorescentiae axillares pauciramosae floribus satis numerosis compositae, rhachibus teretibus sparse puberulis, pedunculis usque ad 9 cm longis, ramulis sec. ad 3 cm, tert. ad 0,5 cm longis. Pedicelli teretes 0,5—1 mm longi cum bracteis bracteolisque late triangularibus 0,5 mm longis calycibusque sparse puberuli. Flores 5-meri 3 mm longi. Calyx late cupuliformis circ. 1 mm alta, lobis triangularibus obtusis tubo aequilongis. Petala oblongo-ovata inflexo-apiculata glabra. Stamina 10, filamentis subulatis 2 mm longis, antheris oblongis 0,5 mm longis. Discus annularis 10-lobis 0,5 mm altus glaber. Pistillum glabrum 1,5 mm altum basi disco cinctum ex ovario ovoideo circ. 1 mm alto, stylo brevissimo et stigmate 5-lobo compositum.

Typus: Bang 2370 in U.S. Nat. Herb. 1380537.

Distributio: Bolivia, dept. La Paz, flum. Yungas, Coroico, Bang 2370 (Aug. 1894, flor.).

Protium Bangii Swart resembles *P. ovatum* Engl., recorded also from Bolivia, but the latter differs mainly by the flattened and bisulcate interjuga, by the shortly acuminate leaflets with 8—10 pairs of sec. nerves, branched halfway the blade and by the 4-merous flowers in clustered inflorescences.

P. Bangii Swart differs from *P. laxiflorum* Engl. by its 2-jugate leaves and by its short petiolules and its leaflets narrowed distinctly to the apex and provided with an acumen 1½ times as long as wide.

Protium decandrum March. var. **breviacuminatum Swart** nov. var. Folia 2-juga, foliolis elliptico-oblongis plerumque 12,5 cm longis 6 cm latis, acumine marginibus parallelis latitudine longitudini subaequali.

Typus: L. Williams 10242 in U.S. Nat. Herb. 1459412.

Distr.: Venezuela, Aragua, El Limon, L. Williams 10242.

Protium juruense Swart n. sp. Arbor circ. 20 m alta. Ramuli robusti 5 mm diam. laeves glabri caesio-brunnescentes lenticellis parvis inconspicuis muniti. Folia 3- vel 4-juga interdum 2-juga 25—35 cm longa ubique glabra, petiolis semiteretibus 5—6,5 cm longis, interjugis carinatis 3—5 cm longis, petiolulis semiteretibus canaliculatis utrinque incrassatis foliolorum lateralium 12,5 (10—17) mm longis foliolorum terminalium circ. 30 mm, foliolis oblongis plerumque apicem versus attenuatis 9—19 cm longis 4—6,5 cm latis terminalibus paulo latioribus lateralibus subobliquis basalibus quam

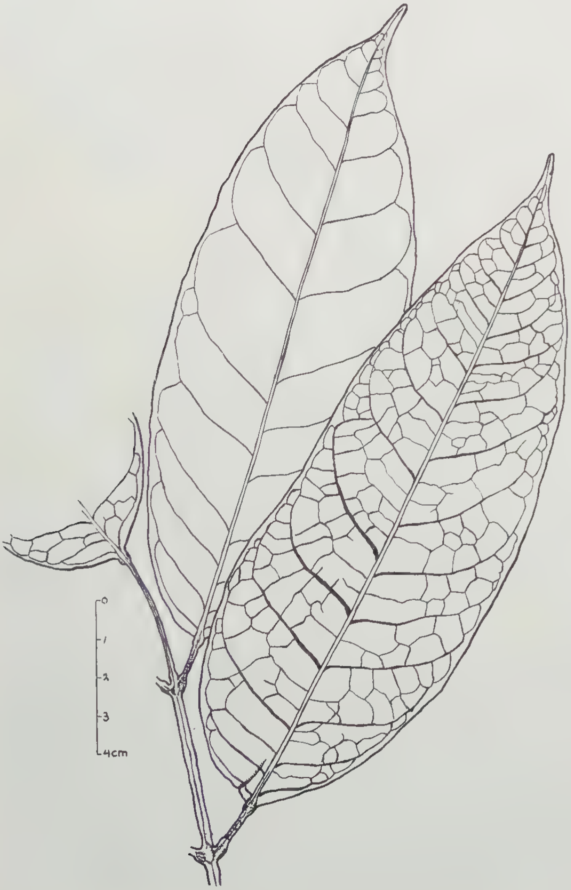

Fig. 1. *Protium juruense* Swart. — Krukoff 5012 in herb. Utrecht 15776A

alia brevioribus, foliolorum omnium apicem versus gradatim in acumen attenuatum 10 (5—20) mm longum 3 (2—3,5) mm latum obtusum angustatis, basi late cuneata, margine integro, subcoriaceis laevibus supra nitidis glaucescentibus subtus opacis, nervis sec. utrinque 12—13 nervis prim. et sec. prominentibus tert. prominulis. Inflorescentiae axillares thyrsoideae pauciramosae petioli foliorum suffulcientium dimidia breviores usque ad 3 cm longae ubique glabrae. Rhaches teretes striatæ leaves. Pedicelli teretes, fructiferi 3—5 mm longi. Flores 5-meri. Calyx cupuliformis lobis semiorbicularibus acuminatis tubo aequilongis. Discus annularis glaber. Ovarium stigmate sessili. Drupa ovoidea rubra apice acuta 1,75 cm longa 1,25—1,5 cm diam.

Typus: Krukoff 5012 in herb. Utrecht 15776A.

Distr.: Brasilia, Amazonia, flum. Jurua, prope ostium flum. Embira, Krukoff 5012 (Jun. 1933, fruct.).
Nom. vern.: almisca.

Protium juruense Swart resembles *P. cuneatum* Swart, *P. laxiflorum* Swart and *P. Bangii* Swart. It differs from *P. cuneatum* Swart by its smaller leaves and by the acumen of its leaflets being 3 times as long as wide, from *P. laxiflorum* Engl. by its larger leaves, its inflorescences being about half as long as the petioles and from both by its lateral leaflets, not narrowed to the base, but to the apex, which is gradually narrowed in a tapering acumen. From *P. Bangii* Swart it differs by its 3- to 4-jugate and larger leaves with longacuminate leaflets and by its short inflorescences.

Protium meridionale Swart n. sp. Arbor circ. 20 m alta. Ramuli robusti 6 mm diam. teretes striati glabrescentes castanei lenticellis oblongis ferrugineis sparsis. Folia 2- vel 3-juga 32 (22—38) cm longa, petiolis semiteretibus basi incrassatis 6,5 (4—9) cm longis cum interjugis petiolulis costis foliolorum facie inferiore sparse appresse puberulis, interjugus carinatis ad nodos incrassatis 3 (2—3,5) cm longis, petiolulis foliolorum lateralium semiteretibus 12 (8—15) mm longis petiolulis foliolorum terminalium teretibus 30 (20—35) mm longis, foliolis elliptico-oblongis plerumque 16 cm longis 6 cm latis terminalibus basim versus angustatis lateralibus apicem versus paulo angustatis foliolis basalibus tamen brevioribus et subovatis, apice foliolorum omnium abruptius acuminato, acumine paulo attenuato obtuso 5 (3—7) mm longo 3 (2—4) mm lato, basi cuneata, margine integro repando, chartaceis laevibus glabris supra nitidulis infra opacis, nervis sec. utrinque 14—16 nervis omnibus prominentibus glabris nervo medio subtus excepto. Inflorescentiae axillares interdum pseudoterminales thyrsoideae pauciramosae circ. 7 cm longae floribus in glomerula terminalia structura dichasialia congestis. Rhaches teretes cum bracteis bracteolisque parvis triangularibus pedicellis teretibus brevissimis necnon calycibus densiuscule appresse puberulae. Flores 4-meri 2,5—3,5 mm longi. Calyx cupuliformis 1,25 mm altus lobis triangularibus tubo aequilongis. Petala elliptico-oblonga glabra apiculo acuto inflexo margine papillosa. Filamenta late subulata in fl. masc. 0,5 mm longa, antherae ellipticae 0,5 mm. Discus annularis 8-lobus glaber. Pistillum in fl. masc. 0,35 mm altum ex ovario globoso 4-lobo et stigmate 4-lobo subsessili compositum.

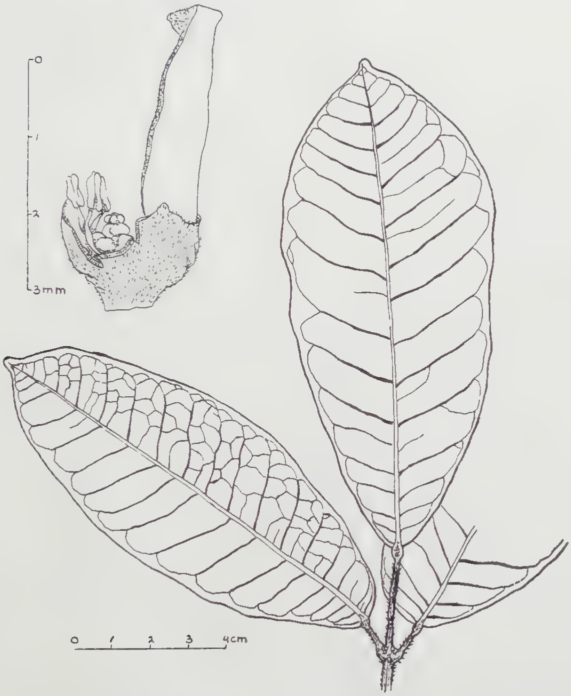

Fig. 2. *Protium meridionale* Swart. — Krukoff n. 10877 in herb. Utrecht 55879A

Typus: Krukoff 10877 in herb. Utrecht 55879A.

Distr.: Bolivia, dept. La Paz, prov. Larecaja, Tuiri, ad ripas flum. Mapiri, Krukoff 10877 (Sept. 1939, fl. masc.); id., prov. S. Yungas, flum. Bopi, San Bartolome, prope Calisaya, Krukoff 10231 (Jul. 1939); id., id., Krukoff 10232 (Jul. 1939).

Protium meridionale Swart resembles *P. ecuadorense* Benoist em. Swart, but the latter differs mainly by the acumen of its leaflets being 3 times as long as wide and by its distinctly pedicellate flowers with a glabrous calyx.

Protium montanum Swart n. sp. Arbor 15—20 m alta. Ramuli graciles 4 mm diam. glabri laeves fusci lenticellis ferrugineis sparsis. Folia 2- vel 3-juga 17,5 (14—20) cm longa ubique glabra, petiolis semiteretibus basi paulo incrassatis 3,5 (2,5—4) cm longis, interjugis semiteretibus 3 (2—3,5) cm longis, petiolulis semiteretibus utrinque subincrassatis longitudine decima parte foliolorum metientibus 6—10 mm longis, petiolulis foliolorum terminalium teretibus 20 mm longis, foliolis oblongis forma irregularibus 7,5 (6—9) cm longis 3 (2,5—3,5) cm latis, terminalibus basin versus paulo angustatis lateralibus asymmetricis, apicem versus abruptius acuminatis, acumine attenuato ipso obtuso 3—6 mm longo 2—4 mm lato, basi cuneata, margine integro subrepando, pergamentaceis laevibus supra viridibus infra pallide viridibus, nervis sec. utrinque 12—13 cum nervis prim. utrinque prominulis, nervis tert. vix conspicuis. Inflorescentiae axillares thyrsoideae laxae e floribus satis numerosis compositae usque ad 4 cm longae. Rhaches teretes cum pedicellis teretibus gracilibus circ. 2,5 mm longis bracteis bracteolisque triangularibus 0,5 mm longis, calycibus sparse adpresse puberulis. Flores 4-meri 2,5 mm longi. Calyx cupuliformis circ. 1 mm longis lobis tubo aequilongis late triangularibus acutis. Petala ovato-triangularia acuta inflexo-apiculata extus pilis nonnullis sparsa margine papilloso. Stamina in fl. masc. 1,25 mm longa, filamentis subulatis 1 mm longis, antheris ellipticis. Discus annularis 8-lobus glaber 0,25 mm altus. Pistillum in fl. masc. circ. 0,5 mm altum, ovarium rudimentarium disco cinctum sparse puberulum stigmate subsessili 4-lobo coronatum.

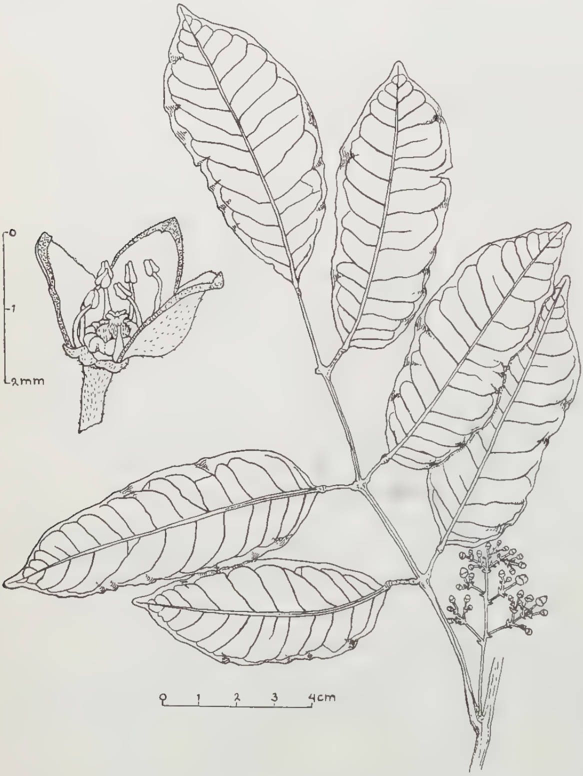

Fig. 3. *Protium montanum* Swart. — Krukoff 11014 in herb. Utrecht 55836A

Typus: Krukoff 11014 in herb. Utrecht 55836A.

Distr.: Bolivia, dept. La Paz, prov. Larecaja, Tuiri, prope Mapiri, Krukoff 10915 (Sept. 1939, fruct.); id., id., Copacabana, Krukoff 11014 (Nov. 1939. fl.

masc.); id., id., Krukoff 11071 (Nov. 1939); id., id., Krukoff 11269 (Nov. 1939, fl. masc.).

Protium montanum Swart resembles *P. giganteum* Engl., *P. nodulosum* Swart, *P. crenatum* Sandw., *P. octandrum* Swart and *P. decandrum* March. *P. giganteum* differs from *P. montanum* Swart by its larger leaves, by its leaflets with 16 pairs of sec. nerves and a linear acumen and by its densely pilose calyx and corolla. *P. nodulosum* Swart differs by its larger leaves, by the linear acumen of its leaflets, by its 10—17 cm long inflorescences and by its 5-merous flowers with densely pilose calyx and corolla. *P. crenatum* Sandw. differs by the serrate margin of its leaflets and its long inflorescences. *P. octandrum* Swart differs by its 1- to 2-jugate leaves and its clustered inflorescences, *P. decandrum* by its 1- to 2-jugate leaves and its 5-merous flowers.

Protium unifoliolatum Engl. var. **inconforme Swart** nov. var. Folia plerumque 1-juga 19—27 cm longa, petiolis semiteretibus 2—4 cm longis, petiolulis lateralibus 0,5—1 cm longis terminalibus 2,5—4,5 cm longis, foliolis lanceolatis apicem versus angustatis lateralibus 12 (9—14) cm longis 3,5 (2,75—4) cm latis terminalibus majoribus 17,5 (16—20) cm longis 4,5 (4-5,5) cm latis omnibus apicem versus gradatim acuminatis, acumine sublineari 7,5—10 mm longo 2—2,5 mm lato obtuso, margine remote sed distincte serrato.

Typus: Gardona 1327 in U.S. Nat. Herb. 1906078.

Distr.: Venezuela, Amazonas, Sierre Parima, flum. Siapa, Cardona 1327 (Mar. 1946, fl. masc.); id., flum. Casiquiare sup., Capihuara, L. Williams 15698 (Maio 1942, fruct.).

Trattinickia Lawrancei Standl. var. **bolivianum Swart** nov. var. Folia minora, petiolis 5—6,5 cm longis, interjugis 2—2,5 cm longis, petiolulis 3—5 mm longis, foliolis 8,5—14 cm longis 2,75—5 cm latis, acumine 8—10 mm longo 3—5 mm lato instructis, basi subcordata, nervis secundariis utrinque 16—18.

Typus: Krukoff 10767 in herb. Utrecht 56926A.

Distr.: Bolivia, dept. La Paz, prov. Larecaja, Tuiri, prope Mapiri, Krukoff 10767 (Sept. 1939, flor.); id., id., Krukoff 10889 (Sept. 1939, fruct.).

Trattinickia rhoifolia Willd. ssp. **Sprucei Engl.** var. **pubescens Swart** nov. var. Petioli, petioluli, nervi primarii utrinque dense nervi secundarii sparse ferrugineo-hirtelli.

Typus: Krukoff 11112 in herb. Utrecht 55967A.

Distr.: Bolivia, dept. La Paz, prov. Larecaja, Copacabana, Krukoff 11112 (Nov. 1939, fruct.); id., id., Krukoff 11229 (Nov. 1939, fruct.).

STUDY OF A PEAT PROFILE ON THE FRISIAN COAST OF THE FORMER "ZUIDERZEE"

BY

M. VROMAN (Utrecht)

Received Dec. 15th, 1951

INTRODUCTION

On both sides of the watercourse, which connects the harbour of Makkum with the "IJselmeer", a wide expanse of low-lying land is found, which follows the Frisian coast. This is the "Makkumer Waard", whose soil profile forms the subject of this study. The soil samples were taken in the so-called "Zuidwaard", which lies to the south of the watercourse. Under a layer of young sea sand extending to a depth of about 2½ m, a two meter thick peat layer was found, which according to the Geological Map belongs to the large peatbog that at one time extended over all Friesland, Groningen and Overijsel.

The subsoil proved to consist of postglacial sand.

STRATIGRAPHICAL AND PALYNOLOGICAL DATA

a. *Stratigraphy*

Below the level of — 4.55 m [1] the soil consists everywhere of sand in which shells of *Hydrobia ulvae*, rests of *Carex*, *Eriophorum*, *Phragmites* and *Calliergon* and a few pieces of *Alnus* wood were found. The transition from sand to peat takes place at about — 4,55 m, but for the next 10 cm the peat still contains an admixture of sand and clay. In this clayey peat we found shells of *Hydrobia ulvae*, *Foraminifera* and *Cardium edule*, remains of *Calliergon* spec., *Leptodictyum riparium*, *Sphagnum* cf. *fuscum*, *Sph. imbricatum*, *Carex* and *Eriophorum*, and also a fragment of a *Salix* stem. We must assume therefore that the area lay at the beginning below sea level, but that the influence of the sea water gradually decreased so that peat formation became possible.

From — 4,45 m to — 3,85 m the peat consists mainly of *Carex*, *Phragmites* and *Eriophorum* rests. We also found in this part wood of *Betula*, a leaflet of *Calliergon giganteum*, and seeds of *Scirpus*, *Ranunculus flammula*, *Carex*, *Menyanthes trifoliata* and *Nymphaea alba*. The microscopical investigation revealed the presence of numerous *Diatomeae* (*Pennatae*) and of *Chara* (— 4,50 m to — 4,30 m).

The next section consists almost entirely of rests of *Scheuchzeria*, but fragments of *Leptodictyum riparium* and *Sphagnum* cf. *cuspidatum* were also met with.

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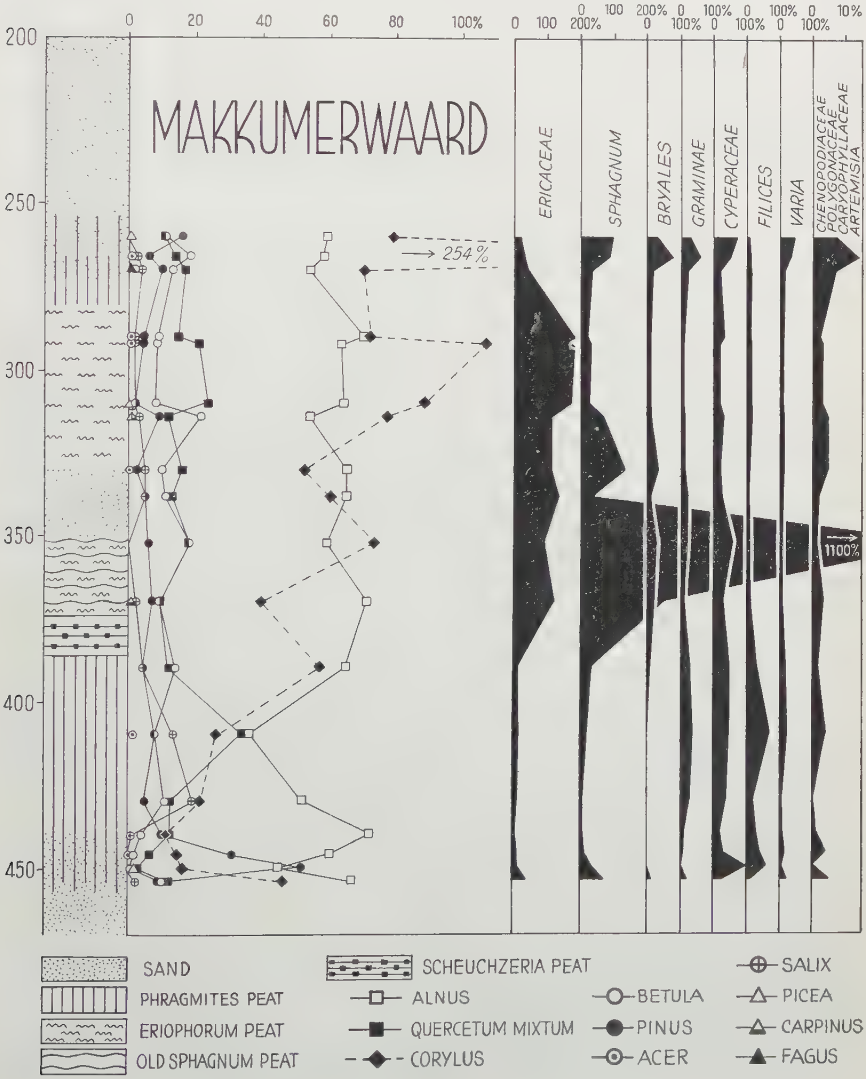
[1] All depths are given with regard to the average sea level as found at Amsterdam.

From — 3,75 m to — 3,50 m the peat is built up of *Eriophorum.* The palynological investigation revealed the presence of numerous *Sphagnum* spores (1100 % at — 3,52 m). We must assume therefore that the submersion was followed by a period in which the soil gradually grew drier, and in which it lost a good deal of its mineral content. This created the conditions for the development of a high-moor vegetation.

According to Tesch (12) and Polak (10) it is not necessary to assume a regression, for the succession marine deposits → *Phragmites* peat → *Carex* peat → *Sphagnum* peat can be explained in another



way. In their opinion the last glacial period was followed by a single continuous transgression. Tesch thinks that in the beginning of the Atlanticum the coherence between England and the continent was broken, and that during the rest of this period the Dutch coast stood under the influence of the tides. The Channel current would have transported large amounts of sand so that in front of the Dutch coast a long series of sand banks were formed. The gaps between these banks would finally have been closed, and so the shorewall would have arisen on which the sea dunes were formed. In the area behind the shorewall the salt was gradually washed out by the water of the rivers and by the rain, and when the soil once more began to subside *Phragmites* peat and, when the mineral content became very low, even *Sphagndm* peat could be formed.

The explanation given by Tesch and by Polak can not be fully correct, for Van Veen (15) could show that practically no transport of sand in a northerly direction has taken place and Baak (1) proved that the sand by which the old sea dunes were built up, did not come from the Channel coast, but from the sea bottom. For this reason it seems improbable that the gradual growth of the shorewall in an easterly and northerly direction should be due to sea currents.

Another explanation was given by Timmermans (13), who proved by means of experiments that a series of sand banks may arise on account of the action of breakers, and that these sand banks may subsequently be united into a shorewall. The old sea dunes might have arisen on a shorewall that owed its origin to a long series of sand banks, which were formed in this way during the Atlantic period. In order that dunes may develop, it is, of course, necessary that the shorewall rises above the level of the sea, so that the sand can dry out and becomes suitable for transport by wind. As was shown for the English Fenlands by Godwin (5) and for the area of NW-Germany by others (summary by Dewers —3—), there must have been a temporary standstill in the transgression or even a regression, and this will have led to the formation of the old sea dunes and to this same cause the transition (in the middle of the Atlantic period) from marine deposits to *Sphagnum* peat must be due.

The formation of *Sphagnum* peat came to an abrupt end on account of a new and sudden transgression. The latter was responsible for the layer of sand and clay that was deposited on top of the *Sphagnum* peat. This time there was no gradual transition between the peat on the sand deposit. The sand itself was marine, as is proved by the presence of *Hydrobia ulvae*.

Rests of *Phragmites*, *Eriophorum* and *Sphagnum imbricatum* and a branchlet of *Calluna* were also found.

From — 3,30 m to — 3,00 m we again have peat, first with *Eriophorum* and *Sphagnum* cf. *cuspidatum* and at a higher level with *Eriophorum* only. The quick transition from sand to *Eriophorum* peat seems to indicate a regression.

Upwards of — 3,00 m the samples prove to contain an admixture of sand and clay and above — 2,60 m the peat disappears. The clay and the sand contain a fair amount of fragmented plant rests, among we recognized *Phragmites*, much *Sphagnum imbricatum* and *Sphagnum* cf. *cuspidatum*. Numerous marine animals were also present, viz. much *Hydrobia ulvae*, one specimen of *Hydrobia stagnalis*, several species of *Foraminifera*, *Cardium edule* and a shell of *Rissoa membranacea*.

Upwards the samples become more and more sandy. This indicates a third marine transgression.

b. Palynology

The palynological investigation showed that the whole peat layer must have been formed in the Atlantic and Subboreal period (see the diagram).

The lowermost samples already contained more *Alnus* than *Pinus* pollen. At — 4,50 m however, *Pinus* reached a higher value than *Alnus*, but such a *Pinus* top is not unexpected in an Atlantic peat bog, for it was also observed by other investigators, e.g. by OVERBECK & SCHMITZ (9), SCHUBERT (11), BRINKMANN (2) and MULLER & VAN RAADSHOOVEN (7).

OVERBECK and SCHMITZ (9) and also SCHUBERT (11) and BRINKMANN (2) point out that their marine formations show everywhere a strong increase of the *Pinus* curve accompanied by a strong decrease of the *Alnus* curve, but that the pollen percentages of the other trees remain constant.

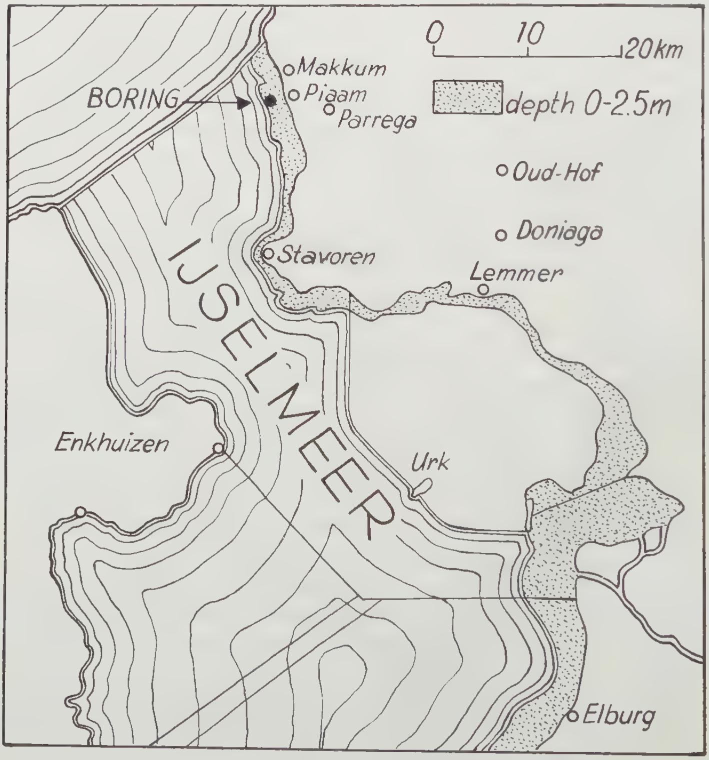
They are of opinion that these changes reflect a shifting of the woodcovered area under the influence of the transgressions. The alders, which grow mainly on bog peat, suffer first and then the long-distance transport of the coniferous pollen comes to the fore. This hypothesis finds support in the fact that the *Pinus* top is always accompanied by the appearance of *Picea* pollen, which disappears as soon as the percentage of the *Pinus* pollen begins to decrease. Differences in resistence to corrosion are according to OVERBECK & SCHMITZ in their diagrams of no importance, for if they were, the pollen of the deciduous trees would have suffered much more than the *Pinus* pollen, but this is not so. That these differences play no part, is, however, no general rule, for in some other instances they must apparently have played an important rôle.

SCHUBERT (11) found in soil samples from Bremervörde that the decrease of the *Alnus* pollen percentages was accompanied by a decrease in the pollen percentages of the other deciduous trees, and that the alder remained therefore the most frequent deciduous tree. Among the pollen of the various kinds of deciduous trees also a selection took place: *Quercus* pollen appeared to decrease much more than that of *Tilia*, which is very resistent. SCHUBERT ascribes his findings to differences in resistance to corrosion.

In the Makkum profile the decrease in the pollen percentages of deciduous trees that accompanies the Pinus top, appears for every kind of tree, to be proportional to its previous value. For the mixed oakforest we found 1 *Quercus* and 2 *Tilia* pollengrains. At — 4,46 m, where we still have 31,3 % of *Pinus* pollen, there were 4 *Quercus* and 6 *Tilia* pollengrains. If SCHUBERT is right, then the high *Pinus* values found in the lower part of the marine deposits at Makkum will probably be due to differences in the resistance against corrosion. The two other transgressions, which evidently also led to the formation of marine deposits, are not reflected in the course of the *Pinus* curve. MULLER & VAN RAADSHOOVEN (7) found at Urk a *Pinus* curve with the same general trend.

The Subboreal period probably begins in the diagram at — 3,10 m. MIKKELSEN (6) has in his diagram of Lake Even, Dalinge Gd. Bp. 21 (Denmark) also three *Corylus* tops; the second corresponds with the beginning of the Subboreal period, the third with the end of this period.

The Doniaga diagram given by FLORSCHUETZ (4) shows exactly the same character. At Doniaga, and also at Parrega, the peat formation stopped before the beginning of the Sub-atlantic period;



but at Oud-Hof it went on in the latter. FLORSCHUETZ is of opinion that this happened not only at Oud-Hof but everywhere in the south-western part of Friesland. When the area was submerged by the water by which afterwards the clay layer was deposited, the younger *Sphagnum* peat began to drift and was finally carried off. For Makkum too this seems to be the most plausible explanation, for the corroded peat rests found above — 3,00 m contain large amounts of *Sphagnum imbricatum*, and this species plays the most important part in the formation of the younger *Sphagnum* peat. It is possible that the younger *Sphagnum* peat has been washed away in historical time, viz. in the thirteenth or the fourteenth century, when the "Zuiderzee" was formed. After the peat had been washed away, the younger sea sand was deposited.

According to VEENENBOS (14) this explanation, which was also brought forward by MULLER & VAN RAADSHOOVEN (7) is unsatisfactory. He points out, that further inland, where the influence of the inundation will have been very slight, with few exceptions (i.a. Oud-Hof), no younger *Sphagnum* peat is to be found. Therefore he thinks it more probable that the formation of *Sphagnum* peat during the Subatlanticum was confined to a limited number of localities.

The *Corylus* values found at Makkum are very high (254 % at — 2,65 m). This high percentage may partly be due to the presence of *Myrica* pollen, which cannot be distinguished with certainty from *Corylus* pollen.

DISCUSSION

MULLER & VAN RAADSHOOVEN (7) found in profiles from the North-eastern Polder indications for the presence of two transgressions in the Atlantic period. They regard the deposits formed during the first transgression (the *Unio*-clay phase) as an offshoot of the old blue sea clay. The *Unio*-clay was deposited in a basin, which had a narrow entrance at Urk. Up to Urk the deposits are more or less marine, but the deposits in the basin itself must have been formed in brackish or in fresh water (the sediment came from the west, the fresh water from the east). After the period in which the *Unio*-clay was formed, the influence of the transgression decreased and peat formation once more became possible. On the *Unio*-clay grew a *Phragmites* peat, which in its turn passed into *Sphagnum* peat. Along the border of the basin, where from the beginning of the Atlantic period the formation of *Carex* peat had continually gone on, now also *Sphagnum* peat was formed. The influence of the transgression therefore gradually decreased (perhaps even some regression may have taken place). The formation of peat in the period following the *Unio*-clay phase was at the end of the Atlanticum suddenly interrupted by a fast and violent transgression (the *Cardium*-clay phase). The *Sphagnum* peat passed into *Phragmites* peat and the latter was covered by a layer of clay. The clay had a strong marine character. This transgression too was suddenly ended: at Urk *Sphagnum* peat was formed almost directly on the clay and at Schokland the Atlantic peat bog was overgrown by wood.

This sudden regression took place before the beginning of the Sub-atlanticum and was followed by a period of more gradual transgression, during which the peat was washed away and the "Zuiderzee" came into being.

Van Zeist (16) found at the "Princehof" (in Central Friesland) also two narrow clay bands that must have deposited during the Atlantic period. Between these clay bands a transition from *Phragmites* peat to *Sphagnum* peat was met with. From the thinness of the clay bands Van Zeist concludes that the transgressions must have reached in this region their farthest point. In these clay bands he found high values for the pollen of *Compositae*, *Chenopodiaceae*, *Caryophyllaceae* and *Graminae*, which indicates a halophytic vegetation.

Veenenbos (14) found that the transgression acquired towards the end of the Atlanticum a greater speed, but that it was finally stopped and made place for a regression. This regression was used by Wassink to explain the horizont of Weber. The faster the lowering of the groundwater level took place, the more the composition of the Subboreal peat approached to that of Weber's horizont.

In the border area of the NE. Polder there is no difference in aspect between the Atlantic and the Subboreal peat, which means that the environment in which in these two periods peat was formed, differed but little. For this reason Veenenbos is of opinion that the lowering of the groundwater level caused by the regression can not have been very important.

The absence of an important fall of the groundwater level in the Subboreal is due to the low level of the basin of the "Zuiderzee", in which several streams poured out their water, and to the narrowness of its connection with the sea.

The data obtained from the Makkum profile agree very well with what was found by the investigators mentioned above.

We now can compare our data also with the results obtained by other investigators who occupied themselves with the area round the North-sea.

Godwin (5) found for the Fenlands that the transgression came to a stop in the middle of the Atlantic period and may even have made place for a small regression and that in the Subboreal undoubtedly a regression took place.

In the coast area of NW-Germany the postglacial transgression was several times interrupted.

Schubert (11) found at Kehdingen a peat layer between the marine sediments. He explains this by assuming a standstill of the transgression, and he dates this standstill in the middle of the Atlanticum. Shortly before the beginning of the Subboreal a regression began.

Schuette (Dewers —3—) published in 1937 a curve representing the movements of the sea level. On account of the presence of a dark coloured clay layer with *Phragmites* rests which he found intercalated between marine deposits in a profile from Norderney, he came to the conclusion that about the middle of the Atlanticum a regression must have taken place.

Brinkmann (2) found a more or less similar situation at Sehestedt. Both investigators moreover noted a regression in the Subboreal period.

Since the beginning of the Atlanticum the sea level in England, in Holland and in NW-Germany must therefore have undergone the following changes:

1. From the beginning to the middle of the Atlantic period a rise.
2. About the middle of the Atlanticum a slowing down of the rise (Godwin, Schubert) and perhaps even a fall (Schuette, Brinkmann).
3. In the later part of the Atlanticum a new and very rapid rise.
4. In the Subboreal period an important fall, which already began towards the end of the Atlanticum.
5. After the Subboreal period a slow rise, which was in several places responsible for the removal of the younger *Sphagnum* peat.

SUMMARY

The subject of this study are soil samples taken in the "Makkumer Waard", a wide expanse of low-lying land, which follows the Frisian coast. Stratigraphical and palynological investigations showed that in the beginning of the Atlanticum the area lay below the level of the sea, but that gradually the influence of the sea decreased and peat formation became possible. From the transition from marine deposits to *Sphagnum* peat (— 4,55 m to — 3,50 m) we must conclude that there has been a temporary standstill in the transgression, or even a regression, in the middle of the Atlanticum. Towards the end of the Atlantic period a sudden marine transgression followed, which deposited a layer of sand and clay on the *Sphagnum* peat (— 3,50 m to — 3,30 m).

Shortly before the beginning of the Subboreal (which probably sets in at — 3,10 m) an important regression began and an *Eriophorum* peat was formed directly on the clay (— 3,30 m to — 3.00 m).

It is probable that the peat formation went on in the Subatlanticum, but the younger *Sphagnum* peat is no longer present, for a third marine transgression, which lead to the formation of the "Zuiderzee", washed away the peat and deposited the younger sea sand.

The data obtained from the Makkum profile proved to agree very well with the results of other investigators who worked in the area round the North-sea.

REFERENCES

1. Baak, J. A., 1936. Regional Petrology of the Southern North Sea. Diss. Wageningen.
2. Brinkmann, P., 1934. Zur Geschichte der Moore, Marschen und Wälder Nordwestdeutschlands. III. Das Gebiet der Jade. Engl. Botan. Jahrbücher *66,* 370.
3. Dewers, F., 1941. Das Alluvium. Geologie und Lagerstätten Niedersachsens, dritter Teil, Känozoïcum. Schriftenreihe der Wirtschaftwissenschaftlichen Gesellschaft zum Studium Niedersachsens. N.F. Bd. 3.
4. Florschütz, F., 1941. Palaeobotanische bijdrage tot de oplossing van het schalterprobleem van de Friesche Weiden. Tijdschr. Nederl. Heide Mij *53,* no. 12.

5. Godwin, H., 1945. Coastal peatbeds of the North sea region, as indices of land- and sea-level changes. The New Phytologist Vol. 44, no. 1.
6. Mikkelsen, V. M., 1949. Praestø fjord. Dansk Botanisk Arkiv. Bind 13, no. 5.
7. Muller, J. en B. van Raadshooven, 1947. Het holoceen in de Noordoostpolder. Tijdschr. Kon. Ned. Aardr. Gen. LXIV, 153—185.
8. Overbeck, F., 1934. Bisherige Ergebnisse der botanischen Moorforschung zur Frage der Küstensenkung an der deutschen Nordsee. Abhandl. Naturwissenschaftl. Verein zu Bremen Bd. XXIX, Heft 1/2, 48—73.
9. Overbeck. F. und H. Schmitz, 1931. Zur Geschichte der Moore, Marschen und Wälder Nordwestdeutschlands. I. Das Gebiet von der Niederweser bis zur unteren Ems. Mitteilungen d. Prov. stelle für Naturdenkmalpflege Hannover, Heft 3.
10. Polak, B., 1936. Pollen- und Torfanalytische Untersuchungen im künftigen Nordöstlichen Polder der Zuiderzee. Rec. d. trav. bot. néerl. XXXIII, 313—332.
11. Schubert, E., 1933. Zur Geschichte der Moore, Marschen und Wälder Nordwestdeutschlands. II. Das Gebiet an der Oste und Niederelbe. Mitteilungen d. Prov. stelle für Naturdenkmalpflege Hannover, Heft 4.
12. Tesch, P., 1935. De vorming van de Nederlandsche duinkust. Groningen.
13. Timmermans, P. D., 1935. Proeven over de invloed van golven op een strand. Leidsche Geol. Mededelingen. T. VI, afl. 3, 231—386.
14. Veenenbos, J. S., 1950. De bodemgesteldheid van het gebied tussen Lemmer en Blokzijl in het randgebied van de Noordoostpolder. Diss. Wageningen.
15. Veen, J. van, 1936. Onderzoekingen in de Hoofden in verband met de gesteldheid der Nederlandsche kust. Nwe Verhand. Bataafsch Genootsch. Rotterdam, 2e Reeks, 11e Deel.
16. Zeist, W. van, 1950. An investigation into the earlier vegetation of Central Friesland (the Netherlands). Rec. d. trav. bot. néerl. XLII, 27—39.

A PALYNOLOGICAL INVESTIGATION OF THE LOWER PEAT IN THE PROVINCE OF FRIESLAND, THE NETHERLANDS

BY

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Up till now the lower deposits of peat (in Dutch: veen-op-grotere-diepte = peat at greater depth) have been investigated in the Netherlands mainly in the Western part of the country, viz. in the provinces of Noord-Holland, Zuid-Holland and Zeeland. The analyses have shown that the development of this, now comparatively well known peat layer must have begun either in the second half of the boreal period or else in the beginning of the atlantic one, and that it must have come to an end in the first half of the latter. Among the earlier investigators the botanist Mrs Vermeer–Louman and some geologists had arrived at the conclusion that the sudden transgression of the North sea which made an end to the formation of peat, took place in the boreal period, and that the whole lower deposit of peat, therefore, was of boreal age (lit. 7). This opinion, however, was sufficiently disproved by Florschütz, and all subsequent analyses have confirmed the view that the peat formation must have stopped early in the atlantic period (lit. 2, 3, 4). The same conclusion was arrived at by Godwin as a result of his investigations of the lower peat found in SE England (lit. 5, 6) and by several German investigators as a result of their analyses of the lower peat, found in NW Germany.

Only one analyses of the lower peat in the province of Friesland, in the Northern part of the Netherlands, has sofar been published. The geologist van Andel found near Kiesterzijl, at a depth of only 3.50 m a thin layer of peat. He identified it with the lower peat from the W part of the Netherlands which occurs several meters deeper. His two diagrams show a boreal age for the basal layers and an atlantic age for the top ones and they confirm therefore the conclusions,obtained in the W part of the country (lit. 1).

During the month of June, 1950, a number of deep borings have been carried out on the territory of the large municipality of Barradeel in the province of Friesland. These borings have been made possible by a grant from the Frisian Academy at Leeuwarden, by the assistance of the department for the maintenance of dikes, roads, bridges and canals in the Province of Friesland and by that of the board of the

Wieringermeer. We wish to express here too our deep-felt gratitude for their help.

Some time before these borings were carried out, the second author visited a deep pit, excavated for the construction of a new sluice near Harlingen, just outside the territory of the municipality of Barradeel. Even at the bottom of this 10 meter deep pit the lower peat was not yet reached but there were a few lumps of peat, that had come to light when a number of poles had to be driven in. These lumps have been analysed by Mr K. B. A. Bodlaender. One part of them showed boreal spectra, the other part atlantic ones, which means that there was a complete agreement with the results, obtained by van Andel in Friesland, and by other investigators in Western Holland. The only discrepancy with the description given by van Andel is found in the great difference in depth of the analysed layers. This difference is the more remarkable as the localities are situated only a few kilometers apart from each other and as the surface is quite flat. Our fig. 1 shows a pollen diagram of a sample of lower peat collected in the part of Barradeel that is situated SE of Harlingen. The layer occurs at a depth of 4.30—4.80, is overlain by marine sand and rests on a layer of cover sand that is rich in humus. As the cover sand below the peat shows typical late-boreal spectra, the development of the peat must have begun in the neighbourhood of the transition between Boreal and Atlanticum. A remarkable feature are the high tops in the *Corylus* line, a boreal top of 283 % and a top at the boreal-atlantic transition of even 1170 %. A large part of the area was apparently during that time covered with *Corylus* bush, which must have ousted all the other trees and shrubs. As *Corylus* in contradistinction to *Betula* and other species was not included in the pollen sum of 150 tree pollen grains used for the construction of the diagram, this abundance of *Corylus* pollen caused a rise of the pollen percentage of *Pinus* and of some other trees. A second diagram of the same layer (fig. 2) constructed after *Corylus* had been included in the pollen sum, gives a much better impression of the pollen production of the forests by which the area must have been surrounded. Though it is still usual to exclude *Corylus* from the pollen sum, this shows that it is better included. This is the more desirable as *Corylus* is not at all confined to the shrub layer of the forests. However, a difference between the two diagrams becomes important only when the percentage of *Corylus* pollen is very high.

With regard to the other botanical remains we can give the following particulars: the dark cover sand contained fragments of *Phragmites* and of *Cyperaceae*. The basal part of the peat was rich in drift sand and it contained fruits of *Potamogeton*, *Carex* and *Betula*, wood of *Betula* and remains of stems and roots of *Cyperaceae*. The next 10 cm (4.70—4.60) still contained fruits of *Potamogeton* and *Carex* but in addition to these the remains of *Eriophorum* tufts and much *Alnus* wood. Up to 4.40 the peat was formed by *Eriophorum* rests mixed with *Carex* and with a few leaves of *Sphaguum*. In the upper part of the peat the quantity of *Sphagnum* remains increased considerably, but *Erio-*

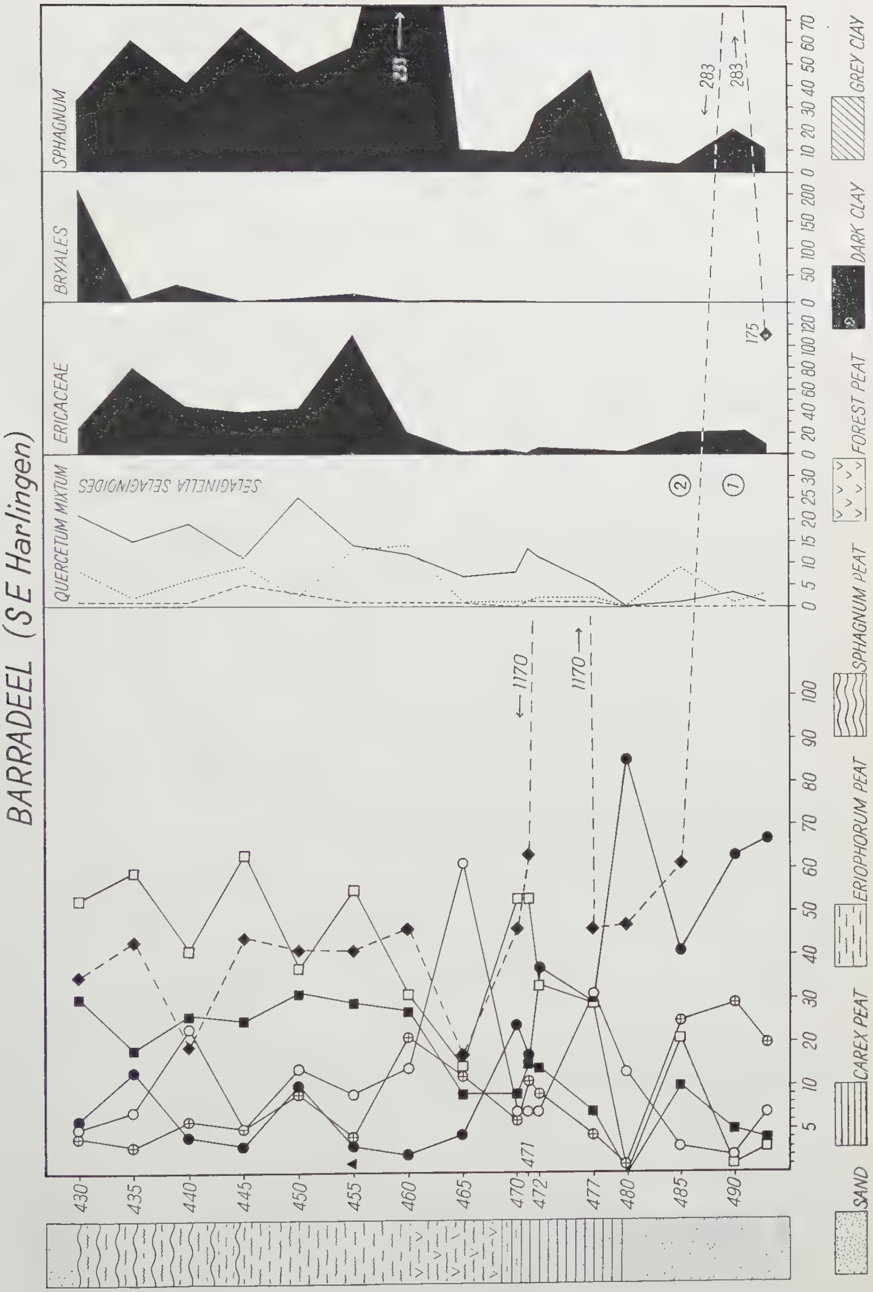
BARRADEEL (S E Harlingen)
SPHAGNUM
BRYALES
ERICACEAE
QUERCETUM MIXTUM
SELAGINELLA SELAGINOIDES
283
283
175
1170
1170
471
①
②
430
435
440
445
450
455
460
465
470
472
477
480
485
490
5 10 20 30 40 50 60 70 80 90 100
0 5 10 15 20 25 30
0 20 40 60 80 100 120
0 50 100 150 200
0 10 20 30 40 50 60 70
SAND
CAREX PEAT
ERIOPHORUM PEAT
SPHAGNUM PEAT
FOREST PEAT
DARK CLAY
GREY CLAY

Fig. 1

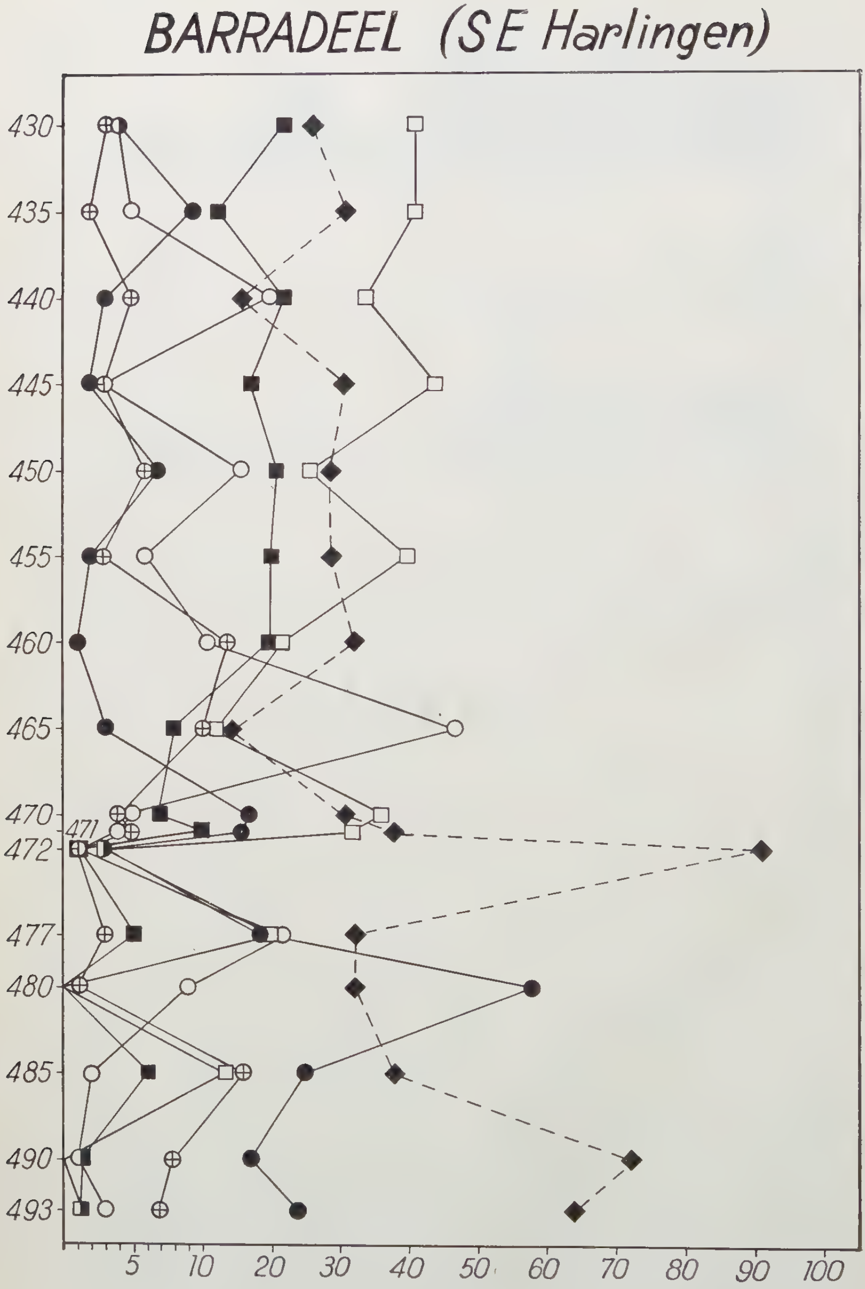
BARRADEEL (S E Harlingen)
430
435
440
445
450
455
460
465
470
471
472
477
480
485
490
493
5
10
20
30
40
50
60
70
80
90
100

Fig. 2

phorum remained an important component; seeds of *Juncus* were found and in the upper 10 cm the peat contained large quantities of fruits and seeds of *Triglochin palustre*. This shows that during the formation of the peat the environment changed from eutrophous to mesotrophous and that it became finally more or less oligotrophous. During the earlier part of the peat formation drift sand was swept into the bog, which shows that even in the Atlanticum the sands were not yet fixed by the vegetation.

Another profile we bored in the part of Barradeel that lies N of Harlingen (see diagram, fig. 3). The peat here occurs at a depth of 590—525. The formation of the peat begun in the latter part of the boreal period and here too the boreal-atlantic transition is marked by a slight indication of a *Corylus* top. The layer of sand rich in humus on which the peat rests, is here much thinner. The peat was formed in a *Carex-Sphagnum* bog; on top of this basal peat layer which contained a good deal of fine sand, we found a thick layer of *Eriophorum* peat, in the upper part mixed with *Sphagnum*, which indicates a change of the environment from the mesotrophous to a more or less oligotrophous condition. In the middle of the peat layer we found in immediate succession indications of two transgressions, each transgression characterized by the succession sand — pale clay — a dark clay that is rich in humus — pale clay — sand. These bands are of marine origin, for we found besides fruits of *Potamogeton* remains of *Ostracoda* and *Foraminifera*, spicula of *Spongiae* and shells of the molluscs *Mytilus edulis*, *Retusa alba*, and *Macoma baltica*. These two transgressions had no influence on the percentages of tree pollen. The percentage of *Sphagnum* spores, however, decreased considerably. The percentage of spores derived from *Bryales* increased from 0 % to 60 %. The possibility that the marine layers have been shoved in during a much later transgression by which the upper part of the peat was separated from the lower part, can not be fully excluded. However, the typical succession of thin sand and clay layers and the decrease in the number of *Sphagnum* spores make it probable that the transgression layers are autochthonous. This means that a temporary breaking in of the sea took place, and that at the end of that period peat formation was resumed.

Fig. 4 shows the pollen diagram of the lower peat near the hamlet of Firdgum, where peat formation began in the vicinity of the transition between Boreal and Atlanticum, recognizable i.a. once more by a *Corylus* top. The layer is 26 cm thick and consists in the basal part of forest peat, formed in an alder brook. The upper 6 cm is pure *Sphagnum* peat consisting of excellently preserved *Sphagnum rubellum* mixed with *Webera nutans* and *Aulacomnium palustre* [1]. This is the more remarkable as the atlantic *Sphagnum* peat (old moss peat) of our raised bogs is always highly humified and shows hardly any recognizable remains of *Sphagnum* plants. CARL ALBERT WEBER, one of the founders of modern peat investigation, was of opinion that the atlantic *Sphagnum*

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[1] We are much indebted to Dr W. MEYER from Amsterdam, now at Bogor (Java), for the identifications of the mosses.

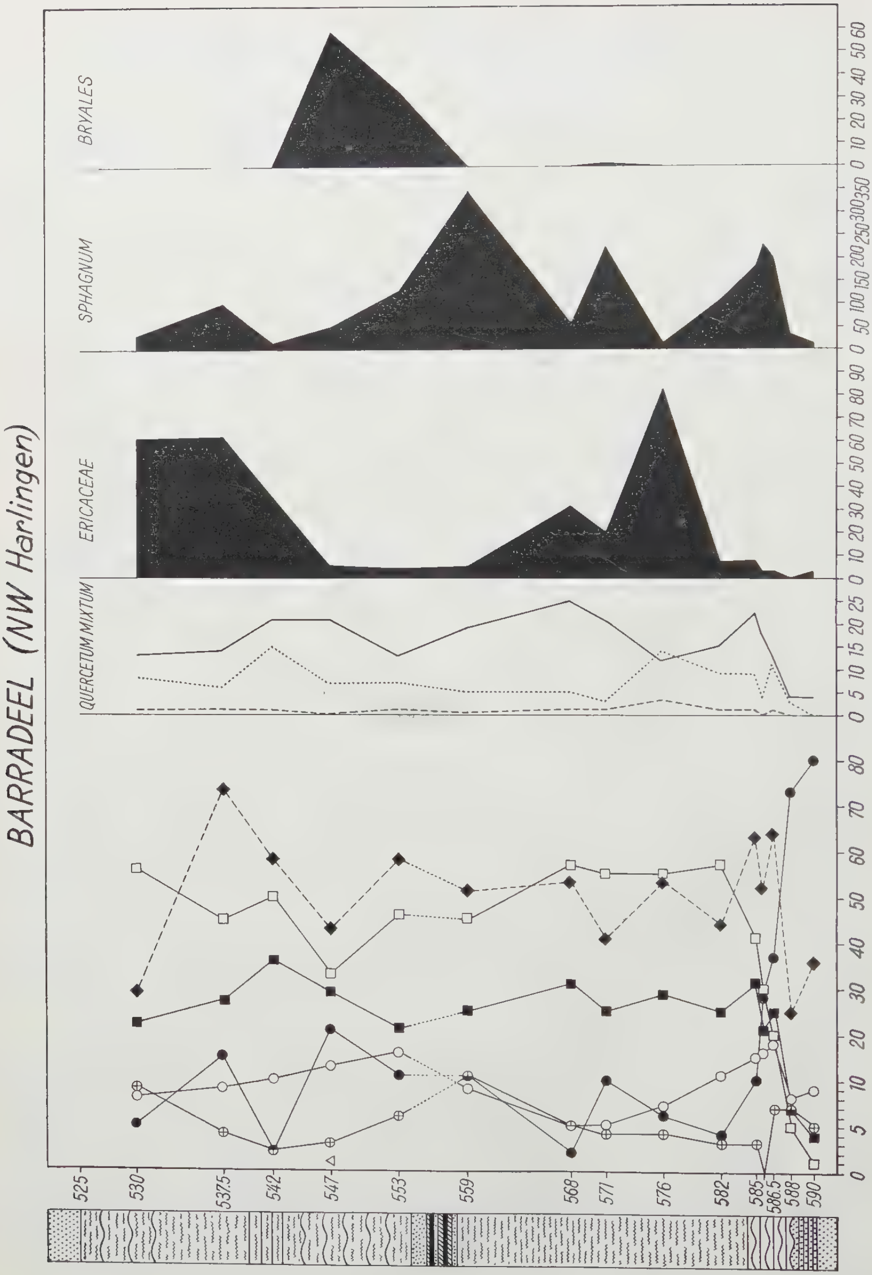
BARRADEEL (NW Harlingen)
BRYALES
0 10 20 30 40 50 60
SPHAGNUM
0 50 100 150 200 250 300 350
ERICACEAE
0 10 20 30 40 50 60 70 80 90
QUERCETUM MIXTUM
0 5 10 15 20 25
0 10 20 30 40 50 60 70 80
525
530
537.5
542
547
553
559
568
571
576
582
585
586.5
588
590

Fig. 3

peat originally must have shown the same appearance as the young (subatlantic) *Sphagnum* peat. In a later and much warmer period, according to him the subboreal one, a decay set in which led to the formation of highly humified peat that we now find in these layers

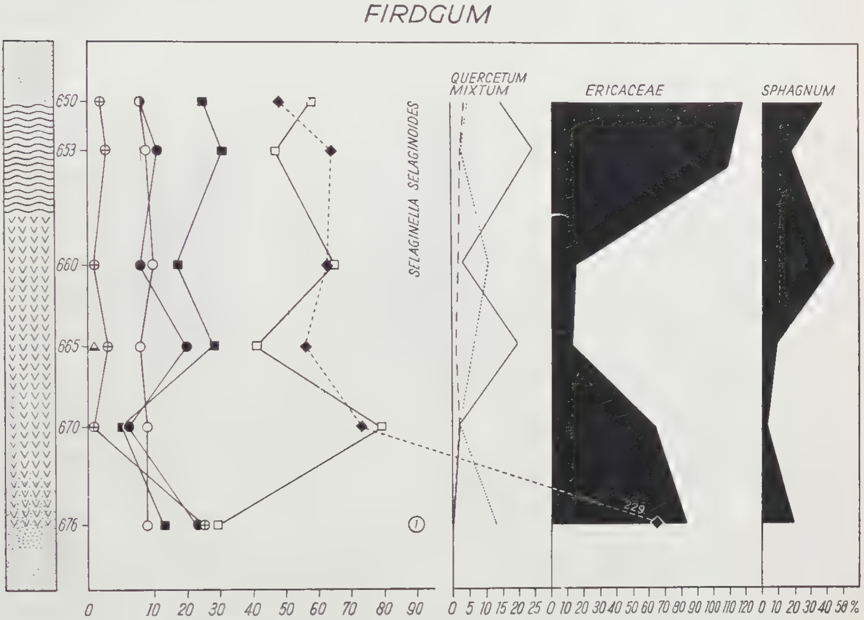

Fig. 4

(lit. 8, 9, 10). Here we found a *Sphagnum* peat covered by marine sands by which already in the atlantic period the supply of air was cut off. The peat consequently did not decay when the peat bog was overflown by the sea. This suggests that the atlantic *Sphagnum* peat too may originally have had the same appearance as the young *Sphagnum* peat and that the decay may have taken place in a later period. Whether this transformation requires a change of climate, as WEBER assumed, is another undecided question.

Below the "Tjummarumer Miedpolder" (see diagram, fig. 5) we found no peat, only a 13 cm thick layer of dark cover sand, rich in humus. Palynological investigation showed that the layer was of boreal age, and corresponded with the boreal sand that we found below the peat layer SE of Harlingen (fig. 1). The lowest spectrum of the diagram, where the sand contained no humus, shows too much secondary pollen to be taken into consideration. The sand contained, just as the sand below the peat layer SE of Harlingen, some microspores of *Selaginella selaginoides*. At this place the peat was probably swept away by the sea, which means that the latter must have worn out a deep channel.

Below the villages Sexbierum and Wynaldum, in the municipality of Barradeel, we found no peat either. Below Wynaldum the marine sands of the tidal flats, by which the peat is usually covered, rested on the boulder clay. This means that all the younger layers must have been swept away by the sea. Below the village of Tjummarum we found only a very thin layer of peat, which proved to be of boreal age. This means either that the top layers of the peat have been eroded by the sea or that the sea already broke in to this area before the latter were formed.

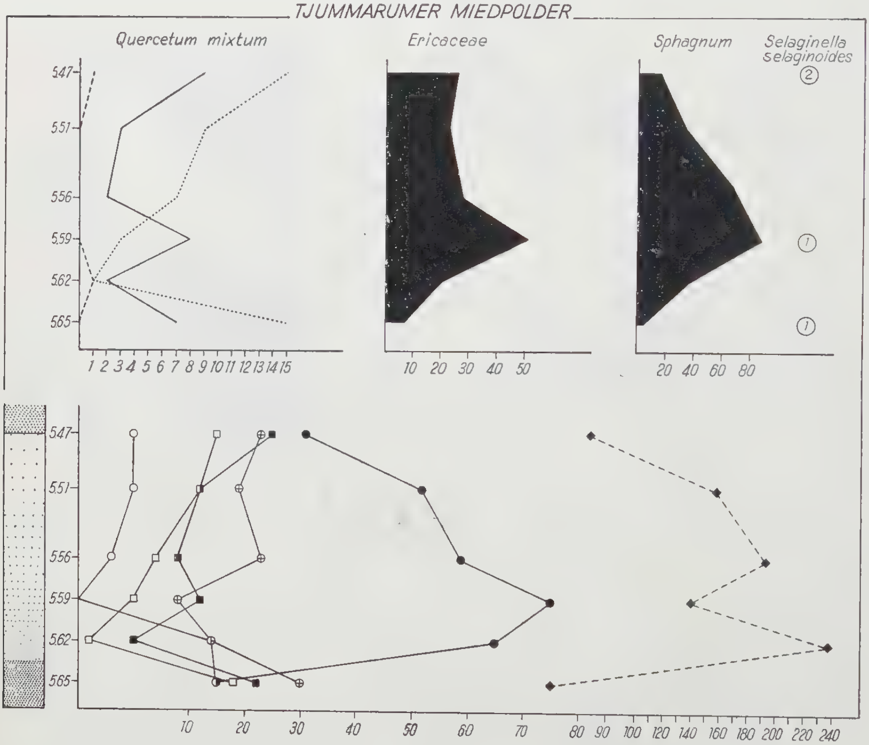

Fig. 5

Our investigations show that in the earlier part of the holocene period a rise of the sea level must have caused a rise of the ground water level: as soon as the ground water reached the surface, the area was covered by plant growth (the dark sand, rich in humus), and peat formation begun. The growth of the peat was made possible by a continuous rise of the ground water level but came to an end when the expanding sea reached the area and the bog was covered by the sands of the tidal flats. In the W part of the country the lower peat developed in a fresh water laguna and the environment therefore was eutrophous to mesotrophous. In our area the circumstances changed during the formation of the peat layers from eutrophous to more or less oligotrophous. The top layers of the lower peat from Firdgum even represent an oligotrophous raised bog, consisting chiefly of *Sphagnum rubellum.*

Peat layers of more recent date have not been met with in our borings. We are as yet unable to give an explanation of the highly varying depths at which the lower peat was met with; in places that were horizontally only a few kilometers apart, the depth at which the peat was found, differs several meters.

REFERENCES

1. Andel, Tj. van, Pollenanalytische datering van een holocene transgressie in Noord-West Friesland; in Geologie en Mijnbouw XI (1949), p. 171—173.
2. Florschütz, F., Bespreking van het proefschrift van Dr C. G. Vermeer-Louman: Pollenanalytisch onderzoek van den West-Nederlandschen bodem; in Tijdschr. Kon. Aardr. Genootsch. (Nov. 1934), p. 1—8.
3. Florschütz, F., Laagterras en "veen op grootere diepte" onder Velzen; in Tijdschr. Ned. Aardr. Genootsch. LXI (1944), p. 25—33.
4. Florschütz, F. en I. M. v. d. Vlerk, Duizend eeuwen geschiedenis van den bodem van Rotterdam; in De Maastunnel II (1939), p. 1—6.
5. Godwin, H., Coastal peat beds of the British Isles and North Sea region; in Journ. of Ecology XXXI (1943), p. 199—247.
6. Godwin, H., Coastal peat beds of the North sea regions as indices of land- and sea-level changes; in The New Phytologist XLIV (1945), p. 29—69.
7. Vermeer-Louman, C. G., Pollenanalytisch onderzoek van den West-Nederlandschen Bodem; Thesis Amsterdam 1934.
8. Weber, C. A., Grenzhorizont und Klimaschwankungen; in Handel. 20e Ned. Nat. Gen. Congr. (1925), p. 260—261.
9. Weber, C. A., Grenzhorizont und Klimaschwankungen; in Abh. Nat. wissensch. Ver. Bremen XXVI (1926), p. 98—106.
10. Weber, C. A., Grenzhorizont und ältere Sphagnumtorf; in Abh. Nat. wiss. Ver. Bremen XXVIII (1930), p. 57—65.

EXPERIMENTS ON THE RETARDATION OF DUTCH IRISES

BY

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With plates VII—VIII

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INTRODUCTION

The normal market of Dutch bulbs lies in the Northern Hemisphere since the successful growing of these bulbs is only possible in those countries where the temperature during winter is not too high. In tropical regions it is not possible to grow normal flowers, unless a low temperature can be provided after planting by artificial means; e.g. by planting the bulbs in pots or boxes and keeping them in cold storage for some months at a temperature in the region of 10°C. (Beijer 1948)

Formerly this same need for a low temperature following planting seemed to prevent the exportation to the Southern Hemisphere, for when sent at the normal time, in September or October, on their arrival in South Africa, South America or Australia the bulbs had to withstand the very high summer temperature prevailing. Planting during this summer period nearly always resulted in failure to flower, and was often followed by total loss of the bulbs.

It became evident later that if it should prove possible to retard the development of the bulbs until March, planting either in this month or early in April would enable them to use the lower soil-temperature which prevails at this time of the year. After a long series of experiments (Blaauw, Luyten en Hartsema 1930, Beijer en Van Slogteren 1933, Van Slogteren 1947, Beijer 1938, 1948) it was proven possible to retard hyacinths, daffodils and tulips until March, or later in the year. For a better understanding of the experiments with irises, the treatments practised in retarding hyacinths, daffodils and tulips will be discussed briefly.

Hyacinth bulbs due to be sent to the Southern Hemisphere are treated as follows: (Van Slogteren en Beijer 1947).

The bulbs are lifted at the normal time, early in July, and kept at a temperature of 30° C. till the middle of October. During this period of high-temperature treatment the flower primordium inside the bulb is slowly developing so that at the end all flowers of the inflorescence are formed. During the following period, from mid-October until the end of December, the temperature is kept at — ½° C. i.e. just below freezing point. In this temperature the development is morphologically practically stopped. One would think now that it would be best to maintain this temperature until planting-time, but it has been proven that bulbs treated in this way, and having been planted in March or April, failed to develop both roots and shoots. Experiments have shown that after the low-temperature treatment a period at a high temperature is again necessary. A temperature of 25½° C. for about 6 weeks or somewhat longer, proved to be optimum. This whole retardation treatment can be indicated briefly as the 30; — ½; 25½-treatment, thus giving the three successive differing temperatures.

The same treatment holds for daffodils (BEIJER 1938).

For tulips another combination of temperatures proved to be necessary and is indicated as the — ½; — ½; 25½ treatment; here we have a long period at a low temperature, ranging from lifting-time in early July until the end of December. During this period the growing point inside the bulb remains dormant. From January onwards at a temperature of 25½° C. this growing point starts developing the flower primordium, and so in the tulip, the flower formation takes place after the low-temperature period; in the hyacinth bulb the flower is formed before the low-temperature treatment.

Late in February, or early in March, the retarded bulbs can be sent to the Southern Hemisphere. They have to be planted as soon as possible after arrival, preferably early in April. They are adapted now to the new climatic conditions and will flower in July or August.

As a matter of course only the southern parts of South Africa, South America and Australia are suitable for the growing of bulbs, for the northern parts of these countries, even during the winter season, have a prevailing temperature, which is too high.

After successful experiments, especially with hyacinths and daffodils, which were followed by their practical application the question arose whether it was also possible to retard bulbs of the Dutch iris. It seemed, however, unrational to apply the retardation treatment used for hyacinths and tulips directly to irises; for iris bulbs behave quite differently from other flower bulbs. In hyacinths and tulips the flower is formed during the time the bulbs are out of the soil, and thus occurs during summer when the bulbs are stored; in daffodils this occurs even earlier, while they are still in the ground, so that after lifting the bulbs the flower formation is nearly completed. In these three bulbous plants, all parts of the flower or inflorescence are present inside the bulb at planting time. After planting it is only a question of growth in length and thickness. This extension growth is greatly influenced by the temperature during the preceding storage-period and, after planting, by the soil temperature. The changing of these temperatures provides us with a means of hastening or retarding the date of flowering.

In the iris, however, the flower formation does not take place during the storage period. In Holland the iris-bulbs are normally lifted in August and planted in October. At that time there is no visible sign of a flower primordium inside the bulb, the growing point being still in the vegetative phase and only splitting off foliage leaves. It is long after planting time, during the winter (November-March) that development of the flower starts. This development thus takes place at a temperature of about 5° C. It is stated (v. d Meulen and Luyten 1936) that during this period temperatures below the freezing point may temporarily arrest the flower formation, without harming later development. The flowering time of the Dutch iris in Holland is strongly influenced by climatic conditions during the spring, but normally the bulbs are blooming at the end of May or early in June.

It seemed questionable whether it would be possible to retard the development of irises in a similar way to hyacinths, daffodils or tulips, since the periodicity of these two groups of bulbs differs so much.

I. Preliminary experiments (1946/47)

The retardation experiments with Dutch irises were started in 1946 with the varieties *White Excelsior* and *Imperator*. The material consisted of first sized bulbs (9 cms in circumference), which were lifted at the end of August. Just as in previous experiments in retarding flower bulbs it proved desirable to divide the whole retardation period into three parts, the first extending from lifting time until the middle of October, the second from mid-October until the end of December or the beginning of January, and the third from the end of December to the middle of February, or somewhat later.

The results obtained with *White Excelsior* will be discussed first. Table I gives the five temperature treatments used. The first treatment is the same as proved satisfactory for tulips; a long period of $-\frac{1}{2}$° C. from lifting time until the beginning of January, followed by $25\frac{1}{2}$° C. during the ensuing six weeks. No. 2 is a continuous storage of the bulbs at $-\frac{1}{2}$° C.

TABLE I

Iris "*White Excelsior*" 1946/47. Application of the five temperature treatments.

No.	Aug. 30—Oct. 16	Oct. 16—Jan. 6	Jan. 6—March. 6
1	$-\frac{1}{2}$	$-\frac{1}{2}$	$25\frac{1}{2}$
2	$-\frac{1}{2}$	$-\frac{1}{2}$	$-\frac{1}{2}$
3	$25\frac{1}{2}$	$-\frac{1}{2}$	$-\frac{1}{2}$
4	$25\frac{1}{2}$	$-\frac{1}{2}$	$25\frac{1}{2}$
5	30	$-\frac{1}{2}$	$25\frac{1}{2}$

Previous experiments for other purposes had shown that low-temperature treatment of iris bulbs often inhibits later flower-formation. The subjection of the bulbs to a high temperature immediately after lifting time proved to be very satisfactory in preventing this inconvenience, and therefore in No. 3 a temperature of $25\frac{1}{2}$° C. is maintained during the first period, and this is followed by $-\frac{1}{2}$° C.

during the two succeeding periods. No. 5, the 30; — ½; 25½ treatment is the same used for the retarding of hyacinths and daffodils. Fearing a detrimental effect of the long period at 30° C. in No. 4, a treatment was added with a temperature of 25½° C. in place of 30° C.

On March 6th, at the end of the third period, the bulbs of all five treatments were kept for four weeks at 17° C. In the experiments with hyacinths, daffodils and tulips, this temperature proved to be very favourable for the resultant quality of the flowers. The bulbs were planted in the open on April 3rd '47 in the experimental fields of our laboratory.

In table II and fig. 2 the flowering results are given, the numbers of the treatments corresponding to those in table I. The photograph clearly shows the total failure of the treatments 1, 2 and 3 and the good flowering results of nos. 4 and 5. Of these two treatments, 30; — ½; 25½ has given 45 flowers out of 50 bulbs or 90 %; and the 25½; — ½; 25½ treatment only 76 %.

TABLE II

White Excelsior 1946/47. Flowering results after temperature treatments 1—5. The bulbs were planted on April 4, 1947; they were stored at 17° C. during the 4 weeks prior to planting.

No.	Treatment	Flowering date	Plants	Flowers	Flower quality	n
1	— ½; — ½; 25½	July 22	18 %	12 %	very poor	50
2	— ½; — ½; — ½	—	0 %	0 %	—	50
3	25½; — ½; — ½	June 6	6 %	6 %	very poor	50
4	25½; — ½; 25½	July 1	86 %	76 %	excellent	50
5	30; — ½; 25½	July 1	100 %	90 %	excellent	50

The two rows of percentages in this and subsequent tables all refer to the total number of bulbs planted. Thus, 6 % in no. 3 indicates that only 6 per cent of the bulbs came up and that all these plants flowered.

From these experiments it seemed clear that only treatment 30; — ½; 25½ could promise good retardation results in sending iris bulbs to the Southern Hemisphere. Moreover, the condition of these bulbs at the end of the treatment early in March, was excellent. They were quite firm and showed neither signs of shooting nor swelling of the root initials.

Some test-shipments to South America gave good results especially with the varieties *Imperator* and *White Excelsior*, but this means of retarding iris bulbs soon turned out not to be the trustworthy method we had expected. In the first place in our trials the method proved suitable for only some varieties of iris, such as *Imperator* and *White Excelsior*, whilst well known varieties, such as *Wedgwood* and *Blue Triumphator*, gave very poor results (see table III, lower part). Secondly after being retarded the variety *White Excelsior* sometimes showed the same abnormal development as *Wedgwood*.

As already mentioned, the preliminary trials of 1946/'47 were also made with *Imperator*. Just as with *White Excelsior* treatments no. 1, 2 and 3 on table I gave almost total failures; no. 4 (25½; — ½; 25½) was worse, while no. 5 (30; — ½; 25½) proved even better than with *White Excelsior*. The results of the latter two treatments are given in table III.

It is seen from this table that a further modification in the method of retardation was added. In this treatment no low temperature was used, but during the whole storing period from September 5th 1946 to March 1947 a constant temperature of 25½° C. was maintained. Just as after the 30; — ½; 25½ treatment the percentage and the quality of the flowers were very good. The date of flowering, moreover was 10 days later, which showed that an even better retardation of the bulbs had been attained.

It seemed desirable to continue the experiments with this treatment and to compare it with the 30; — ½; 25½ treatment. It was also thought necessary to follow the morphological development during the process of retardation to discover at which time eventual abnormalities originated.

TABLE III

Flowering results of some varieties of Dutch iris following various retardation treatments. *Imperator* was planted on April 3, 1947, the two other varieties on April 6, 1948.

Treatment	Flowering date	Plants	Flowers	Flower quality	n
Imperator					
25½; — ½; 25½	July 5	37.5 %	32.5 %	medium	80
30 ; — ½; 25½	July 4	100 %	98 %	excellent	50
25½; 25½; 25½	July 14	100 %	96 %	excellent	50
Wedgwood					
30 ; — ½; 25½	July 4	44 %	12 %	poor	50
Blue Triumphator					
30 ; — ½; 25½	July 14	34 %	18 %	poor	50

The percentages refer to the total number of bulbs planted.

II. THE HIGH-TEMPERATURE RETARDATION TREATMENT (25½° C.) AS COMPARED WITH THE COMBINED HIGH- AND LOW-TEMPERATURE TREATMENT (30; — ½; 25½)

In order to understand the morphological changes occurring during the retardation treatment it is necessary to know something of the normal structure of the iris-plant (see also BLAAUW 1935). A first sized bulb e.g. of the variety *Imperator*, is surrounded by three thin brown-coloured tunics. The greater part of the bulb consists usually of 4 white coloured very thick fleshy bulb scales. At flowering time 2 or 3 scale leaves or sheating leaves, surrounding the underground part of the stem, are emerging from within the innermost bulb scale, generally just reaching the ground level. Normally this stem is bearing 9—11 foliage leaves, the phyllotaxis being distichous. The two uppermost leaves, differentiated as the valves of the spathe, envelop the flower bud.

The experiments were started as soon as possible after the bulbs had been lifted and cleaned. In these freshly harvested bulbs the sheath leaves and 4 or 5 of the leaf primordia were already split off by the growing point.

Table IV shows the length of the outermost leaf and the number of foliage leaves (in brackets) at successive dates during the retardation treatment. The variety *Wedgwood* was chosen for giving consistently bad results after the 30; — ½; 25½ treatment, when compared with *Imperator*. First sized bulbs were used.

When retarded for flowering in the Southern Hemisphere, the retardation is stopped at the beginning of March, but in this experiment the bulbs were left at 25½° C. much longer in order to find out how long the temperature of 25½° C. could be maintained without it causing damage to the young growing plant inside the bulb.

TABLE IV
Length of the outermost foliage leaf in mm and the total number of leafprimordia formed (in brackets). n = 5.

Wedgwood 1948/49	Sept. 11	Jan. 12	March 7	Apr. 13	May 13
30 ; — ½; 25½	7.9(5.0)	8.8(5.8)	19.6(8.2)	**25.0(9.8)** *	**33.6** *
25½; 25½; 25½	7.9(5.0)	17.0(6.6)	21.1(6.6)	31.1(8.0)	34.1(8.0)
Imperator 1948/49	Sept. 13	Jan. 14	March 7	Apr. 14	July 14
30 ; — ½; 25½	2.7(4.6)	5.9(5.8)	10.4(7.0)	11.7(6.8)	**21.7(9.3)**
25½; 25½; 25½	2.7(4.6)	8.8(6.4)	11.1(7.0)	14.5(7.8)	17.5(8.8)
Wedgwood 1947/48	Febr. 25				
30 ; — ½; 25½	**25.8(6.8)**				
Imperator 1947/48	Febr. 20			Apr. 13	July 27
30 ; — ½; 25½	8.3(5.6)			**19.2(7.8)**	**20.3(10.4)***
25½; 25½; 25½	10.6(6.2)			13.1(7.0)	20.5 (8.5)

1948 : — ½° C. from Oct. 18 until Dec. 29.
1947 : — ½° C. from Oct. 16 until Dec. 29.
* flower formation started.
Figures in bold-faced type: morphological development abnormal.

As shown in table IV, on September 11th, the date of the commencement of the experiment with *Wedgwood*, the average length of the outermost foliage leaf was 7.9 mm, and there were 5 leaf primordia. Four months later, on January 12th, the length of the leaf after the 30; — ½ treatment, was 8.8 mm, after the 25½ treatment it was 17.0 mm; the number of leaf primordia being 5.8 against 6.6; and the retarding-power of the 30; — ½; 25½ treatment would seem to be the greater. Two months later, however, on March 7th, the difference in length was reduced to only 1.5 mm, whereas the numbers of leaf-primordia were 8.2 and 6.6; so that now the activity of the growing point would seem to be more retarded after the 25½ treatment.

On April 13th all bulbs looked quite normal after the 25½ treatment, but the combined high-low temperature retardation had given rise to an abnormal development of the foliage leaves in many of them, which is indicated in the table by figures in bold-faced type. The growing point, moreover, had stopped the formation of foliage leaves and had passed into the flower-forming phase, which is indicated by an asterisk.

The abnormal morphological structure was characterized by a scale-like swelling of the lower part of the foliage leaves. Later on the tops of these leaves turned brown and became shrivelled, the basic parts developing like true bulb scales, while the young flower primordium perished early. It is evident that such bulbs failed to flower and very often did not sprout at all.

On May 13th the bulbs of the 25½; 25½; 25½ treatment still looked quite normal and even on August 13th, which is not mentioned in table IV, after an eleven month retardation period at 25½° C., although somewhat shrivelled, they showed a normal development, no sign of shoots or root development being visible externally. On this date the length of the outermost leaf was 39.4 mm. and the average number of leaves was 8.8.

In table IV the dates referable to *Imperator* (1948/49) are also given. It seems superfluous to follow step by step the development of this variety after the two retarding treatments. The following conclusions can be drawn from the data of this table. First of all the length of the first foliage leaf on the different dates of examination is much shorter than on the corresponding dates for *Wedgwood*. Secondly, the internal morphology on April 14th after the 30; — ½; 25½ treatment is still quite normal, whereas *Wedgwood* on that date already showed an abnormal structure. Yet *Imperator* in the long run was also damaged by this treatment; for on July 14th some of the bulbs showed the same abnormal development as *Wedgwood* had done, while the 25½; 25½; 25½ retarding showed no damaging influence.

The lower part of table IV gives some interesting data of the same two varieties, though the year is now 1947/1948. After the 30; — ½; 25½ treatment *Wedgwood* as early as February 25th showed an abnormal morphological development in most of the bulbs; *Imperator* as early as April 13th in some of the bulbs only, in both cases much earlier than in 1948/49. The 25½; 25½; 25½ treatment in 1947/48, applied only to *Imperator*, caused no abnormalities in this generally unfavourable year and even on July 27th the morphological development was quite normal.

The main conclusion to be drawn from the data of table IV is that continuous storage of the bulbs at 25½° C. has a much greater retarding effect than the 30; — ½; 25½ treatment. This is particularly due to the absence of any tendency to abnormal morphological development, even in an early flowering variety like *Wedgwood.*

From most of the treatments in table IV samples of about 100 bulbs were planted in the experimental field at Lisse early in April, after having been stored at 17° C. for one month. This planting date was chosen as being about the same planting time as for bulbs sent to the Southern Hemisphere; in addition bulbs from some of the treatments were planted early in May and June. The flowering results of these different lots of bulbs are given in table V.

After the 25½ treatment all samples of *Wedgwood* and *Imperator* flowered very well. The quality of the flowers produced could be classed as either very good or excellent.

The 30; — ½; 25½ treatment, however, proved to be very detrimental for *Wedgwood*; when planted early in April the result was a total failure in 1947/48, with only 12 % flowers of poor quality. This was to be expected for on February 25th (on table IV) the morphological development had already shown abnormal symptoms. In the following season, 1948/49, 92 % of the bulbs planted gave flowers but they were of poor quality.

This accordance between the findings of the morphological examination and the flowering results was also evident in the variety

TABLE V

Flowering results of *Wedgwood* and *Imperator* following various retardation treatments, and different planting dates. All groups were stored at 17° C. for the month prior to planting. n = ± 100.

Wedgwood 1948/49	Date of Planting		
	April 5	May 4	June 1
30 ; — ½; 25½	June 27 (92 %) †		
25½; 25½; 25½	July 3 (100 %) *	July 15 (98 %)	Aug. 1 (100 %)
Imperator 1948/49	April 5	May 4	June 1
30 ; — ½; 25½	July 17 (100 %) *		
25½; 25½; 25½	July 19 (100 %) *	Aug. 7 (100 %) *	Sept. 5 (92 %)
Wedgwood 1947/48	April 6		
30 ; — ½; 25½	July 4 (12 %) †		
Imperator 1947/48	April 6	May 7	June 3
30 ; — ½; 25½	July 17 (95 %) *	July 26 (57.5 %) †	— (0.0 %)
25½; 25½; 25½	July 27 (93.8 %) *	Aug. 3 (100 %) *	Aug. 20 (78 %)

† flowers medium or poor.
* flowers excellent.
otherwise the flowers were good or very good.

Imperator 1947/48, where the abnormal development was first observed on April 13th. The bulbs, stored at 17° C. on March 3rd and planted on April 6th, produced 95 % flowers the quality of which was excellent. Bulbs, however, planted after April 13th, on May 7th, produced only 57.5 % flowers of poor quality, whilst those planted on June 3rd produced no shoots at all.

These flowering results thus provided confirmation of the conclusion already drawn from the morphological examination, viz. that a continuous storage of the bulbs at 25½° C. produces a much better retardation effect than the 30°; — ½; 25½ treatment.

III. The significance of the retardation at 25½° C. for the export of Dutch irises to the Southern Hemisphere

During the years 1948, '49 and '50 retardation treatment at 25½° C. of approximately six months duration, was tested on several varieties of Dutch irises by planting them early in April in the experimental fields of our laboratory; samples of these lots were sent to South America, South Africa and Australia.

For the month prior to planting the bulbs in Holland, a temperature of 17° C. was maintained. Data concerning the well known varieties *Wedgwood*, *White Superior*, *White Excelsior*, *H. C. van Vliet* and *Imperator* are given in table VI, in which the flowering date is given as the time at which most of the flowers were open. The percentage of bulbs planted which produced a normal flower is also mentioned. From the data given it appears that in all cases 96—100 % of the bulbs flowered very well. In the foreground of Fig. 3 *White Excelsior* is shown flowering on July 16, 1949, while behind other groups of flowering irises can be seen. It is remarkable that in the succeeding years the differences between the flowering dates for each variety are rather small.

TABLE VI

Date of flowering and percentage of flowering plants (in brackets) of different varieties of Dutch iris after a six months retardation period at 25½° C. During the last month before planting a temperature of 17° C. was maintained. n = 50 or 100.

Year	Planting date	*Wedgwood*	*White Superior*	*White Excelsior*	*H. C. v. Vliet*	*Imperator*
1948/49	5-4	3-7(100%)*	—	15-7 (98%)*	17-7 (98%)*	19-7(100%)*
1949/50	3-4	28-6 (96%)*	10-7(100%)*	11-7(100%)*	16-7(100%)*	17-7 (96%)*
1950/51	2-4	1-7 (99%)*	14-7 (99%)*	14-7 (98%)*	16-7(100%)*	21-7 (97%)*

* Flowers excellent.

Apart from the varieties mentioned in table VI some yellow varieties were also tested, but although the flowering results were good, too many bulbs were lost early, actually during the retardation treatment.

This loss in bulbs during the high temperature treatment in itself decides whether a variety will be suitable for export to the Southern

Hemisphere or not. Table VII shows the percentages of loss for several varieties in the years 1949, '50 and '51, which were determined early in March about the date of shipping. In most cases the loss remained at a rather low percentage, seldom exceeding 5 %. An exception to this was found with *Yellow Queen*, for here the loss was in the region of 60 %. This variety was unable to stand the long storage at 25½° C., the bulbs drying out too much and the root initials swelling too early. *Golden Emperor* seemed much better, sustaining a loss of only 2.1 %but this yellow variety also proved to be less suitable owing to too great a degree of shrinkage and a too early root development. The bulbs of the other varieties remained quite firm without showing any sign of root growth. The relatively higher losses in 1950 of *Imperator* and *White Excelsior*, are noteworthy, with 5.6 and 10.8 % respectively.

TABLE VII

Percentage loss in bulbs of Dutch irises early in March after a six months retardation treatment at 25½° C.

Variety	1948/49	1949/50	1950/51
Imperator	1.7 % (1200)	5.6 % (1100)	0.5 % (2000)
H. C. v. Vliet	2.1 % (1500)	2.9 % (375)	0.9 % (2000)
White Excelsior	0.9 % (1000)	10.8 % (1000)	1.3 % (2000)
Wedgwood	0.1 % (1500)	0.1 % (1000)	0.2 % (1000)
White Superior	—	—	1.7 % (1000)
Yellow Queen	± 60 % (750)	—	—
Golden Emperor	—	—	2.1 % (1000)

The total number observed is given in brackets.

Since the shipping of iris bulbs to the Southern Hemisphere is the principal aim of these investigations, samples of retarded bulbs were sent to South America, South Africa and the southern part of Australia. Just as in our previous experiments with hyacinths and daffodils, the bulbs were placed in the holds under the waterline to avoid too high a temperature in transit. It soon appeared, however, that the shipping of retarded iris bulbs provided a difficult problem, for, particularly after long sea passages, the bulbs often arrived in a bad condition with both shoots and roots already sprouting. As a matter of course such bulbs either failed to grow at all, or produced only stunted plants with poor flowers.

In order to determine the influence of different temperatures in transit some bulbs from March 1 were kept for six weeks at 25½°, 17°, 9° and 1° C.; the trial was made with *Wedgwood*, this variety being most susceptible to temperature influences at that time. Figure 1 shows the morphological development during the different temperature treatments. On January 12th, after 4 months storage at 25½° C. the average length of the first foliage leaf was 17.0 mms, and on March 1st 21.1 mms, on which date one group of bulbs was left at 25½°, while three other groups were stored for 6 weeks at 1°, 9° and 17° C. respectively. At the end of this period the length of the first leaf at 1° was 28.1 mms, at 25½°, 31.1 mms, at 17°, 41.1 mms, and at

9°, 51.1 mms. Thus storage at 9° or 17° C. caused an extension growth of the leaves to such an extent that after six weeks the shoot had already grown out of the top of the bulb, flower formation had started and the roots had developed too much; and this in dry, well-ventilated storage rooms. It is obvious that the results would have been worse were the bulbs exposed to the same temperature in a damp atmosphere, which possibly occurs during transit.

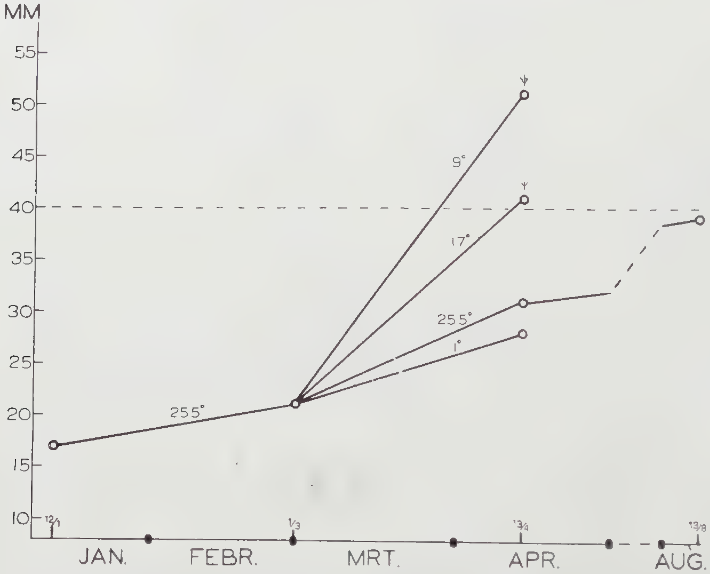

Fig. 1. Iris "*Wedgwood*" 1949. Length of the outermost foliage leaf inside the bulb in mms. Bulbs retarded at 25½° C. from September 11, 1948 until March 1, 1949. Influence of different storage temperatures from March 1, until April 13.
↓ Flower formation started.
The dotted line indicates the average height of the bulb.

It can be seen in Fig. 1 that on August 13th, after a further 4 months storage at 25½° C. the shoot was still within the bulb, its length being only 39.4 mms.

Of the two temperatures ensuring the best conditions for bulbs during transit, that of 25½° C. will not be so easily realised in practice, especially since storage of bulbs at a high temperature necessitates the existence of good ventilation. For this reason 1° C. seemed more promising, whilst retarding the extension growth even more adequately. The bulbs of these two treatments, planted in Holland early in April, flowered excellently, the 25½° bulbs on July 8th, the 1° bulbs on July 4th, both sets bearing 100 % flowers. It remains to be emphazised however, that the flower quality can be affected unfavourably by too long a storage at 1° C. (see also p. 282).

As a result of these trials an attempt was made to have the bulbs shipped in cold storage, but two difficulties now arose. Firstly a temperature of 1° C. was not available, so we had to make do with one which fluctuated between 1—3° C. Secondly, bulbs shipped in this way have to be unloaded and unpacked as soon as possible after arrival, for cooled bulbs once exposed to a higher temperature will become moist, and during later transport, e.g. by rail, are very susceptible to damage by the development of mould.

In 1949 and 1950 many samples of retarded irises were sent to different countries in the Southern Hemisphere.

A survey of the flowering results for both years is given in table VIII, and the results of the four varieties *H. C. van Vliet*, *White Excelsior*, *Imperator* and *White Superior*, were added to simplify matters. The dates of flowering and the percentages of flowering plants produced by the total numbers of bulbs shipped, are given in this table. Flowering results higher than 70 % are in bold-faced type. The shipments are numbered 1—14 [1], partly loaded in cold storage (C), partly under the waterline (W).

The date of arrival and the number of days of transit (in brackets) proved to be very important. All shipments arriving in May (1, 2, 4, 7, 14) being 60—87 days on the way, gave bad results; all except one of the shipments (3) arriving in March or April (5, 6, 8, 9, 10, 11, 12, 13), transit taking 36—58 days gave good results. The shortest transit time with the earliest arrival (11) gave the best results (97.0 %) the longest transit time and the latest arrival (7) gave total failure (3.0 %).

From these facts it is clear that the best results in the Southern Hemisphere are to be obtained by planting the bulbs early in April, and they therefore have to be shipped from Holland about the middle of February. It is also of great importance to ensure that the passage is the shortest possible.

Some shipments were loaded partly in cold storage, and partly under the waterline. Comparison of nos. 8 and 9, and of nos. 12 and 13 shows no great difference between the two sites of loading; both gave excellent results, though the quality of the flowers and the length of the flower stems of the cooled shipments were somewhat better in those bulbs carried in cold storage. After too long a passage, especially with cold storage bulbs which were not immediately unloaded but were kept for some time at higher temperatures or taken by rail to more distant destinations, the results were very bad (1, 7, 14). The bulbs of such shipments were generally damp on arrival, and mouldy, showing long shoots and roots.

In both years the flowering dates in South Africa fell in August, in South America and in Australia in September. The quality of the flowers of the shipments 5, 6 and 8 up to and including 13 was excellent.

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[1] We are very grateful to Mrs A. DE WINTER–FERGUSON (1, 2, 8, 9) at Hurlingham (near Buenos Aires) for all the trouble she has taken with the trial shipments, and for sending us elaborate reports of great value.

The same applies to the following persons: Mr Dr A. J. LOUW (3, 11) Stellenbosch, Mr F. A. VLAG (4, 12, 13) Immerpan, Mr F. M. READ (5) Melbourne, Mr R. W. TURNER (6, 14) Warburton, Mr K. C. HOCKEY (7) Palmerston and Mr. Ir J. ROBERTS (10) Buenos Aires in connection with a shipment to Tucuman.

The numbers in brackets refer to table VIII.

Apart from the four varieties already mentioned, trials were also made with *Wedgwood* and *Golden Emperor*, but these varieties proved to be less suitable, for both developed shoots and roots too easily during transit. This agrees with the data of Fig. 1 which shows the development of a strong extension growth as soon as the temperature happened to sink too far below $25\frac{1}{2}$° C. or to rise considerably above 1° C. *Wedgwood* has occasionally given good flowering results in Australia and South America, but only after a very favourable passage.

TABLE VIII

Flowering results of retarded irises in the Southern Hemisphere. The data refer to the varieties *Imperator*, *H. C. van Vliet*, *White Excelsior* and *White Superior*.

No.	1949		Date of arrival	% Flowers	Date of flowering	n
1	Am.	C.	13-5 (63)	10.0 %	24/9 — 4/10	150
2	Am.	W.	13-5 (63)	48.0 %	9/10—16/10	150
3	Af.	W.	8-4 (41)	40.0 %	18/8 —25/8	250
4	Af.	W.	9-5 (72)	36.5 %	7/8	200
5	Au.	C.	4-4 (44)	**89.6** %	12/9 —20/9	250
6	Au.	C.	6-4 (46)	**80.0** %	12/9 —15/9	350
7	N.Z.	C.	20-5 (87)	3.0 %	—	350
No.	1950					
8	Am.	C.	19-4 (40)	**91.0** %	22/8 —23/9	200
9	Am.	W.	19-4 (40)	**90.0** %	10/9 —30/9	300
10	Am.	W.	24-4 (43)	**71.0** %	15/8	200
11	Af.	C.	30-3 (36)	**97.0** %	2/8 —15/8	200
12	Af.	C.	21-4 (58)	**93.7** %	6/8	300
13	Af.	W.	21-4 (58)	**92.8** %	10/8 —14/8	400
14	Au.	C.	11-5 (60)	28.0 %	10/10—21/10	300

Am.	South America	N. Z.	New Zealand
Af.	South Africa	C.	loaded in cool store
Au.	Australia (southern part)	W.	under the waterline

The number of days in transit after arrival (in brackets) is mentioned.

The percentages refer to the number of flowering plants produced by the total number of bulbs shipped.

One further point of interest remains. Apart from the retarding treatment $25\frac{1}{2}$; $25\frac{1}{2}$; $25\frac{1}{2}$ the combination 30; $25\frac{1}{2}$; $25\frac{1}{2}$ was also applied to all the varieties used. Neither here in Holland, nor in the Southern Hemisphere was any definite difference to be found in the quality of the blooms, the date of flowering or the loss of bulbs. Figure 4 shows flowers of iris "*Imperator*", retarded in this way and planted in Holland on May 4th after one month's storage at 17° C.

IV. THE APPLICATION OF THE RETARDATION TREATMENT TO OBTAIN FLOWERING IRISES FROM MAY UNTIL DECEMBER

The flowering period of the different varieties of Dutch iris is not normally a long one. The retardation experiments, aiming at the export to the Southern Hemisphere, suggested a means of producing flowering irises over a much longer period both in Holland and abroad. The normal planting time of bulbous irises is October or November. The possibility of retarding iris bulbs at 25½° C. for a rather long time makes it possible to delay this planting date until after the winter period. Planting early in April, May or June, as already mentioned in table V, may give flowering plants in July, August and September.

It soon appeared possible to obtain irises flowering continually throughout the entire summer, as is shown in table IX for iris "*Imperator*". The bulbs of this trial were retarded at 25½° C.

From November 7th 1949 until June 6th 1950 3 lots of 50 bulbs were planted each month in the open, after one month's treatment at 9°, 17° and 25½° C. Furthermore early in October, November and December 1949 3 lots were again planted in each month in a non-heated glasshouse. From the blooming dates of table IX, indicating the opening of the first flowers of each lot, it can be concluded that there was a practically uninterrupted period of flowering from May 1st until the end of August. The average number of flowers produced was about 95 % with the temperature at 25½° C. and 97 % with the two other temperatures.

TABLE IX

Flowering dates of iris "*Imperator*" retarded from Sept. 6, 1949 at 25½° C.

Date of planting		Temperature during last month before planting		
		9° C.	17° C.	25½° C.
12-10	I	**1-5**	**7-5**	11- 5
7-11	I	12-5	**13-5**	16- 5
6-12	I	20-5	**21-5**	23- 5
7-11	II	4-6	**6-6**	8- 6
6-12	II	8-6	**10-6**	13- 6
6- 1	II	13-6	**15-6**	20- 6
6- 2	II	20-6	**22-6**	27- 6
6- 3	II	2-7	**4-7**	12- 7
6- 4	II	13-7	**14-7**	22- 7
6- 5	II	31-7	**5-8**	25- 8
6- 6	II	26-8	**28-8**	14-10

I. planted in an unheated greenhouse
II. planted in the open.
Figures in boldfaced type: the best flower quality of the three lots planted on the same date.

From the three temperatures used during the last month prior to planting, 9° resulted in the earliest flowering, and 25½° in the latest. Although very good flowers were produced following all three treatments, the quality of the flowers of 17° nearly always looked somewhat better; and so we find the simplest way in which to obtain a continuous flowering of retarded irises during summer is to plant them about every two weeks, after one month's storage at 17° C. Under normal climatic conditions in Holland the following varieties proved to be suitable for this purpose: *Wedgwood*, *Imperator*, *H. C. van Vliet*, *White*

Excelsior, *White Superior* and if not dried out too much during the 25½° treatment, *Golden Harvest* and *Golden Emperor* can also be included in this list.

The latest possible time for planting in the open in Holland is at the end of June or the beginning of July, with a flowering period in the first part of October. Fig. 5 shows *White Superior* planted on July 3rd and flowering outdoors on October 13th. During this late flowering time damp weather conditions will often stain the blooms, although this may be prevented by the timely use of glass covering. Planting still later in July, results in too late a development, and the plants during autumn are badly damaged by cold and bad weather conditions, without reaching the blooming period. Planting in a glasshouse in July or August proved to be very unsuccessful. The temperature of both soil and air was too high apparently during these months and prevented a normal development of the plants. Only a small number of the bulbs planted reached the flowering stage, and these produced only poor blooms of an inferior quality.

Probably the only way in which to obtain good flowers of retarded iris bulbs after September will be to plant them in forcing boxes; and until now only a few preliminary experiments have been undertaken. The best results were obtained with *Wedgwood*. In 1950 bulbs of 10 cms circumference, retarded at 25½° C., from August 24th 1949 until one month prior to boxing, and kept at 9° C. during this latter month, were boxed in the open on August 13th 1950; and after having been taken to the glasshouse (± 11° C.) on October 31st, they were flowering on November 18th, with 95 % flowers. The following year in 1951, having been treated in a similar way, but taken earlier to an unheated glasshouse, on October 12th, they flowered on October 22nd producing excellent blooms. (n = 200).

As has already been mentioned on page 278 the extension growth of retarded iris bulbs is so intensely stimulated by storing them at 9° or 17° C. that the leaves are early found to be growing out of the top of the bulb and this is especially true of *Wedgwood*. When these bulbs have to be planted on the spot it will not be very dangerous, but when they have to be sent elsewhere, such bulbs will be badly damaged during transit; and in such a case a temperature of 1° C. may be used in place of 9° or 17°. Some data are given in table X, which shows the influence of these temperatures on the blooming date of retarded irises.

It is clear that the earliest flowering is produced after 1 month's storage at 9°, and the latest after one month 1°, but even after late planting (*White Superior* on July 2nd) the difference between the 17° and 1° treatments is not very great. The quality of the flowers with both was excellent, only the flowers of *Wedgwood* planted on June 1st and flowering early in August were somewhat smaller, probably in consequence of the high summer temperature.

This same table (X) shows a very remarkable difference between one month's and two months' storage at 1° C. Bulbs of the iris *H. C. van Vliet* planted on May 1st. flowered with excellent blooms on

August 5th after 1 month 1° C. but when planted on the same date after 2 months at 1°, they flowered as early as July 16th about 3 weeks earlier and with very small and poor flowers. Planting on June 1st gave similar results. A too long storage at 1° C. must be avoided, as it accelerates flowering and produces tenuous plants with poor blooms.

TABLE X

Flowering dates of retarded irises after being treated for one month at 9° C. and 17° C.; or after one and two months at 1° C.

Variety	Date planted	Temperature before planting:			
		1 month 9° C.	1 month 17° C.	1 month 1° C.	2 months 1° C.
Wedgwood '49	5-4	30-6 (98%)*	3-7(100%)*	5-7(100%)*	—
,, ,,	4-5	13-7 (98%)*	15-7 (98%)*	19-7 (98%)*	—
,, ,,	1-6	28-7 (98%)*	1-8(100%)	8-8 (98%)	—
White Superior '50	1-5	23- 7(100%)*	27-7 (100%)*	31- 7(100%)*	—
,, '51	2-7	1-10 (92%)*	13-10 (90%)*	17-10 (96%)*	—
H. C. v. Vliet '50	1-5	—	—	5-8 (96%)*	16-7(98%) †
,, ,,	1-6	—	—	13-8 (100%)*	5-8(94%) †

In brackets: percentage of flowering plants.
Quality of unindicated flowers was good: quality * was excellent: and quality † indicates that flowers were small and poor, and plants spindly.
n in most cases 50 or 60 bulbs.

As mentioned above, it is possible to retard irises long enough to have them in flower till early in November, but on the other hand, bulbs which are lifted in summer can be forced in January after being subjected to a special temperature treatment. Perhaps it will prove possible in future to bridge the remaining period of November and December, and with this in view, the following trials with the irises *H. C. van Vliet* and *White Superior* are worthwhile mentioning. The bulbs of *H. C. van Vliet* were kept at 25½° C. from September 8th, 1949 until August 30th, 1950 and thereafter for one month at 1° C. They were then planted in forcing boxes on September 30th, 1950 and taken to an unheated glasshouse, where the temperature soon became too low; the flowering was thus delayed until May 1951, when 39 bulbs out of 40 produced excellent flowers. (see Fig. 6)

Still more promising were the results obtained with *White Superior*, shown in Fig. 7 flowering on December 12th, 1951, during the final preparation of this publication.

SUMMARY AND CONCLUSIONS

Normally the saleable bulbs of the different varieties of Dutch iris are lifted in August and planted again in October or November. During the time the bulbs are out of the soil they are stored at a temperature of about 23—25½° C. during the first weeks, which is lowered to about 17° in the last weeks before planting.

During this storage period, in contrast to other flower bulbs such as hyacinths and tulips there is no flower formation. After planting, the growing point inside the bulb continues to split off leaf primordia, and it is during the winter at a rather low temperature that the flower formation is started and accomplished.

The flowering period of these irises is rather short, the earliest, such as *Wedgwood*, normally flowers at the end of May, the later varieties in the first part of June.

All experiments on the retardation of irises in the same way as for hyacinths, daffodils or tulips, i.e. by applying low (— ½° C.) or combined high and low temperature treatments (30; — ½; 25½° C.), failed to give satisfying results.

It proved possible, however, to retard iris bulbs excellently by storing them at a constant temperature of 25½° C. This temperature has to be applied as soon as possible after the normal lifting and cleaning of the bulbs.

During this temperature treatment the growing point only continues very slowly to split off leaf primordia, while the growth in length of the foliage leaves is strongly retarded. Iris bulbs retarded in this way are suitable for export to the Southern Hemisphere. Shipped in February-March and planted early in April the bulbs, which are now adapted to the reversed climatic conditions, will flower in August or September.

Temperatures between about 7° and 17° C. must be avoided as far as possible during transport; for these temperatures greatly stimulate the growth of both shoots and roots. Shipping in cold storage at + 1° C. is to be recommended, provided the bulbs are unloaded and unpacked as soon as possible after their arrival.

It must be emphasized that planting early in April will guarantee the best results, which necessitates the bulbs being forwarded in time; moreover the duration of the transport is preferably not longer than six weeks.

Very good results were obtained with trial shipments to South America, South Africa and Australia, which included first sized bulbs of *Imperator*, *H. C. van Vliet*, *White Superior* and *White Excelsior*.

The retardation at 25½° C. could be continued over a still much longer period. Even an early variety such as *Wedgwood* could be retarded from August until September of the following year, when the bulbs were seen to be somewhat shrivelled, but still showed no shoot development externally. Internally the first leaf had just reached the top of the bulb, but the flower formation had not started even yet.

On any given day of this long retardation period it proved possible to plant the bulbs and have them in flower after about three months, or even later depending on the climatic conditions prevailing at the time.

Instead of planting immediately from storage at 25½° C. a better quality of flower could be obtained by storing the bulbs at a temperature of 17° C. for one month before planting.

By planting retarded bulbs in Holland at repeated intervals it has been proven possible to obtain flowering irises in the open from May until October; success being achieved with the varieties *Wedgwood, Imperator, H. C. van Vliet, White Excelsior* and *White Superior*.

Some preliminary experiments have shown the possibility of having flowering irises even later, e.g. in November and December. Retarded bulbs were boxed therefore in August (after 12 months storing at 25½° C.) and transferred later on to a glasshouse, where they were forced at 10—13° C.

REFERENCES

Beijer, J. J. en E. v Slogteren (1933), Preparatie en verzending van bloembollen voor het Zuidelijk Halfrond. Med. Lab. v. Bloemb. Onderz. 46. Weekblad v. Bloembollencultuur. 44.

Beijer, J. J. (1938). Preparatie van Narcissen voor het Zuidelijk Halfrond. Med. Lab. v. Bloemb. Onderz. 61. Kweekersblad 1938.

Beijer, J. J. (1948), Bloeimogelijkheden van bloembollen op het Zuidelijk Halfrond. Med. Lab. v. Bloemb. Onderz. 86. De Tuinbouw p. 317.

Blaauw, A. H., Ida Luyten en Annie M. Hartsema (1930). Verschuiving der Periodiciteit. Med. Lab. Plantenphys. Ond. 28. Verh. Kon. Akad. v. Wetensch. Amsterdam XXVI no. 7.

Blaauw, A. H. (1935), De periodieke ontwikkeling van een boliris. Med. Lab. Plantenphys. Onderz. 43. Verh. Kon. Akad. v. Wetensch. Amsterdam XXXIV no. 3.

Meulen, A. v. d en Ida Luyten (1936), Vergelijking der jonge organen van Spaansche, Engelsche en Hollandsche Irissen. Med. Lab. Plantenphys. Onderz. 49. Verh. Kon. Akad. v. Wetensch. Amsterdam XXXIX no. 7.

Slogteren, E. v. en J. J. Beijer (1947), Aanwijzingen betreffende de behandeling en verscheping van bloembollen bestemd voor het Zuidelijk Halfrond. Lab. v. Bloembollen Onderzoek.

Fig. 2. Iris "*White Excelsior*" on July 2 1947. Flowering results after the temperature treatments No. 1—5 (see table II)
1. — ½; — ½; 25½ 2. — ½; — ½; — ½ 3. 25½; — ½; — ½
4. 25½; — ½; 25½ 5. 30; — ½; 25½
Only Nos. 4 and 5 have produced flowers.

Fig. 3. Iris "*White Excelsior*" flowering on July 16, 1949. Immediately after lifting time, on August 16, the bulbs were stored at 25½° C. until March 1. After four weeks storing at 17° C. they were planted in the open on April 5.

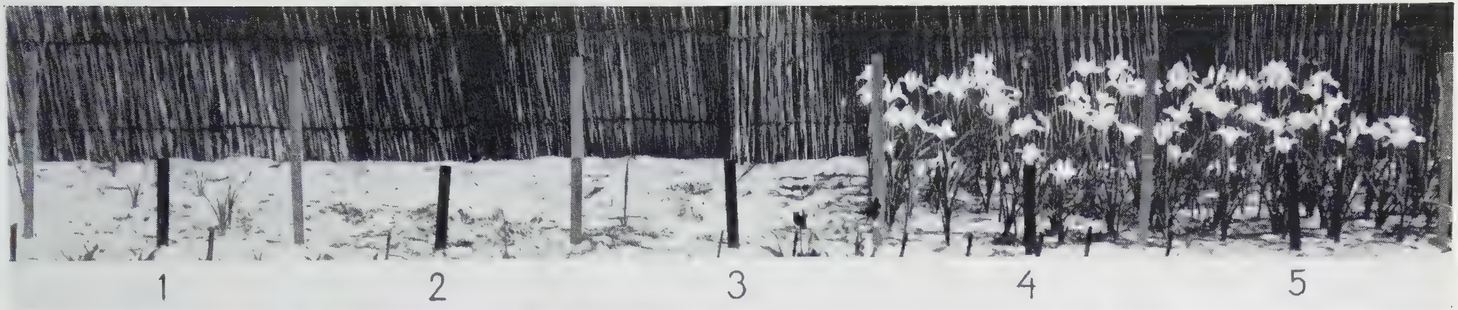
Fig. 4. Iris "*Imperator*", grown outofdoors, flowering on August 6, 1949. Retardation temperature 30° C. from September 8, 1948 until October 18 and 25½° C. until April 4, 1949. Planted on May 4 after one month's storage at 17° C.

Fig. 5. Iris "*White Superior*", grown outofdoors, flowering on October 13, 1950. Bulbs lifted in August 1949 and retarded at 25½° C. Planted on July 3, 1950 after one month storing at 1° C.

Fig. 6. Iris "*H. C. van Vliet*". Bulbs lifted in September 8, 1949, retarded at 25½° C. until August 30, 1950. After one month storing at 1°, boxed on September 30 and put in an unheated glasshouse. The flowering started on May 6, 1951.

Fig. 7. Iris "*White Superior*", flowering at December 12, 1951. Bulbs retarded at 25½° C. from September 13, 1950 until July 4, 1951. Boxed on August 9 after one month storing at 9°. Boxes put outofdoors until October 12; in an unheated glasshouse until November 12. From this date forced at 10—13° C.

Fig. 2



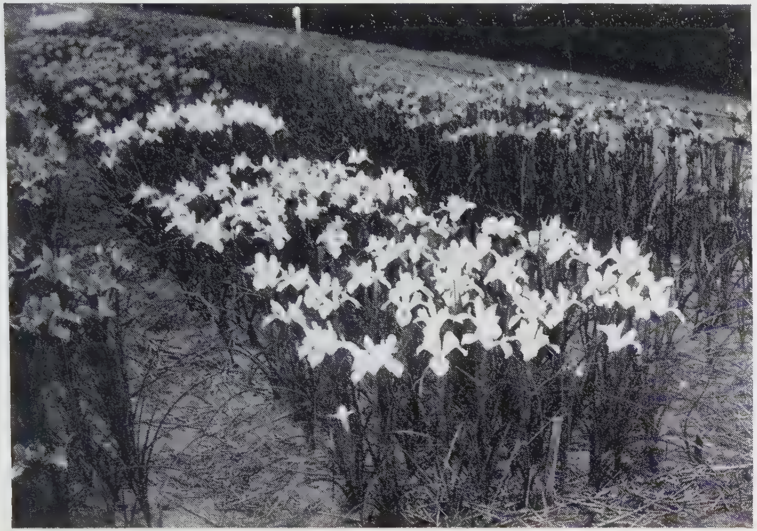


Fig. 3

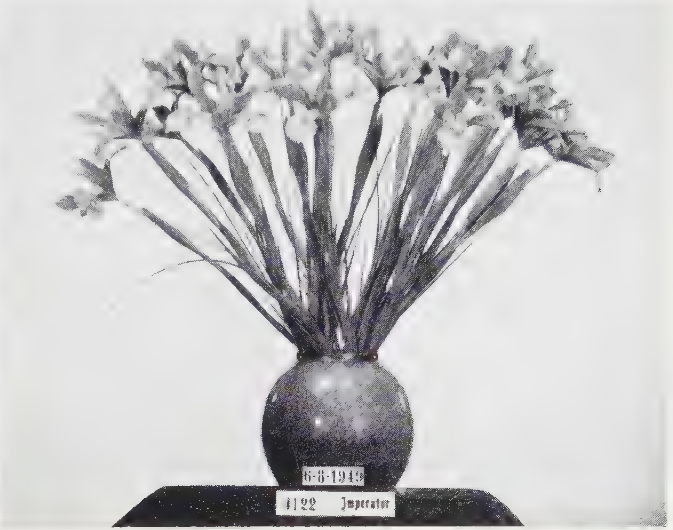


Fig. 4

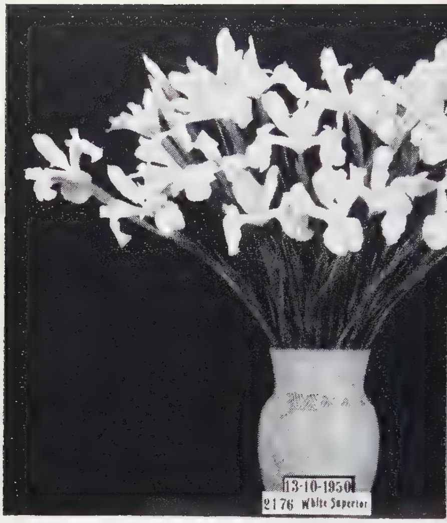


Fig. 5

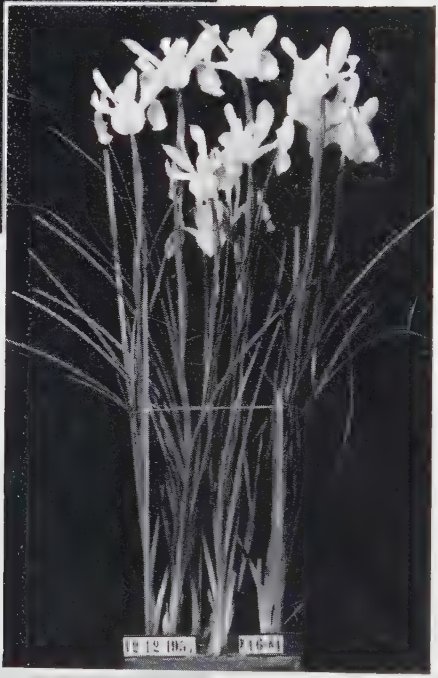


Fig. 7

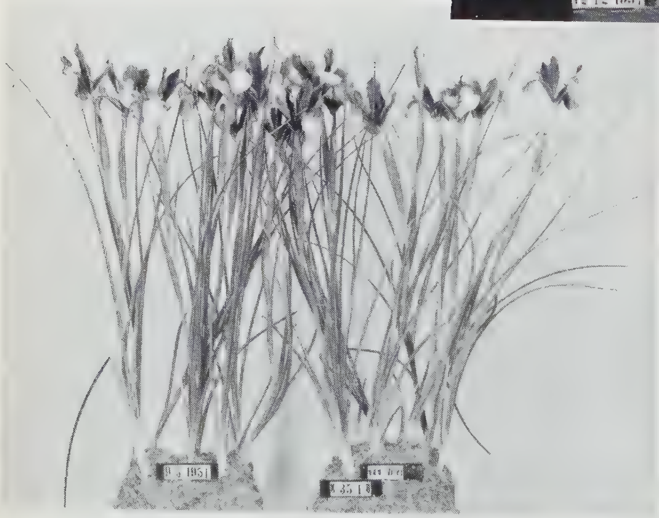


Fig. 6

THE LEAF OF BAUHINIA

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A. INTRODUCTION

In the genus *Bauhinia* three types of leaves occur, *a* simple, *b* butterfly-shaped with a deep incision at the top, *c* bifoliolate, (cf. fig. 1). In most species the leaves belong to type *b*, to which shape some owe their Malay name "kupu-kupu" (butterflies). The resemblance with a butterfly is not confined to the shape, but extends to the way the "wings" are laid together at night.

I intend to treat the following species:

Type *a*. *B. bidentata* Jack., *B. pyrrhaneura* Korth., *B. kockiana* Korth., *B. assuruana* Moric., *B. platycalyx* Benth., *B. cordifolia* Roxb.
Type *b*. *B. flammifera* Ridl., *B. purpurea* L., *B. scandens* L., *B. tomentosa* L., *B. variegata* L., *B. monandra* Kurz and some others. *B. corymbosa* stands close to type *c*.
Type *c*. *B. binata* Blanco, (syn. *B. blancoi* Baker), *B. winitii* Craib., *B. diptera* Bl.

It seems possible to consider the three types as transformations of a single one. The data agree with this. There is a gradual transition between the types. In *B. scandens* L. type *a* and *b* can be found on the same plant, in *B. rubiginosa* Berg., type *b* and *c*. Leaves of all three

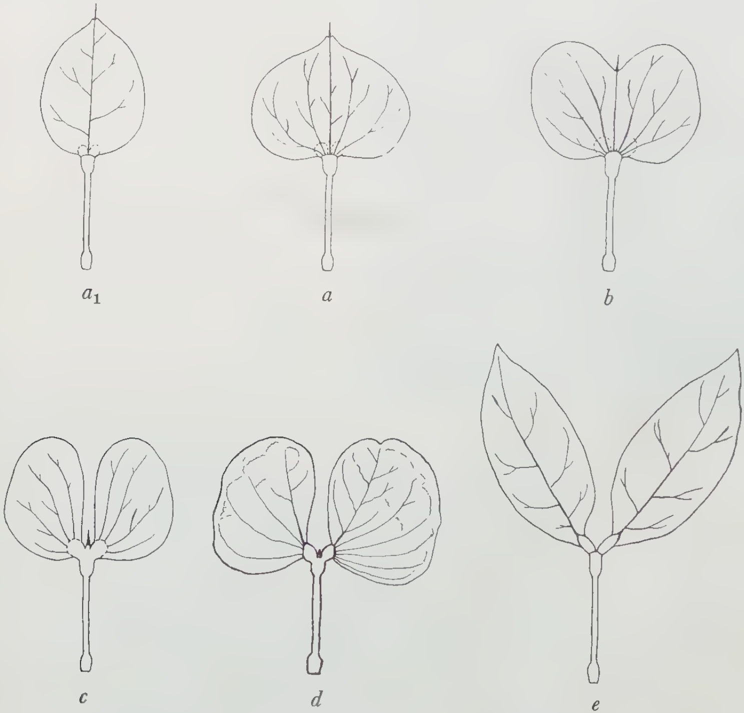

Fig. 1. Types of leaves in Bauhinieae and in Hardwickia;
a_1. Bandeiraea tenuiflora.
a. Simple-leaved type of Cercis, Bauhinia bidentata a.o.
b. Bilobate type of B. purpurea a.o.
c. B. binata a.o. bifoliolate types.
d. Monojugate compound leaf of Hardwickia binata. Different ways of venation combined into one leaf.
e. Trachylobium verrucosum, monojugate compound leaf.

types have the apical incision, though it is very shallow in those of type *a* (cf. fig. 1 and 4).

All three types show a petiole with a basal joint (primary pulvinus) and an apical joint near the lamina (secundary pulvinus). In comparison with other leguminous leaves, type *a* might be called unifoliolate and type *c* bifoliolate. The apical joint is undivided, even in bifoliolate leaves, where both "leaflets" are inserted on it. This joint has been overlooked by many botanists, probably because they used herbarium material, where the swelling is scarcely visible (cf. D, 2). A characteristic trait, common to all types, is the curious bristle (the German "Granne") at the bottom of the incision (in bifoliolate leaves therefore between the "leaflets" on top of the petiole).

Ecologically the three types also have much in common, viz. the tendency to fold up the lamina along the midrib. These nyctinastic movements are executed by means of special motile cushions (laminar joints) one at the base of each half of the lamina. They are distinct from the apical common joint but merge gradually into the rest of the leafblade.

Now the question arises which type is the original one. (The question may be put in the sense of phylogeny or of idealistic morphology).

Is it really true that the "simple" leaf of *B. bidentata* is the basic type from which types *b* and *c* have been derived, either by splitting (as a mere descriptive description may suggest) or by terminal inhibition of growth (pleuroplastic development), to use a more directly comprehensible terminology? An authority on morphology like TROLL has accepted the latter idea in his "Vergleichende Morphologie" (p. 1025 and 1591) and compares the *Bauhinia* leaf to the well known leaf forms of *Ipomoea pes-caprae* and *Lourea vespertilionis*. BREMEKAMP (1) gave in a short note some arguments in favour of this idea.

Other morphologists like URBAN (10), VELENOVSKY (11), UITTIEN (9) and FRIES (2) defended the opposite conception, according to which type *c* would have the original form out of which the simple leaf arose by fusion. WATARI (12) thinks the leaves of *Cercis* and *Bauhinia* can be classed as a case of palmately compound leaves with many leaflets. In two short notes in a popular journal VAN DER PIJL (6, 7) advanced some arguments in favour of fusion, but after the remarks of BREMEKAMP (1) the question must be treated in a more thorough and different manner. I feel justified in doing so now, because I had living material at my disposal, while most of the previous work was done in herbaria only.

It seems hazardous to plead for the possibility of fusion after it has come into discredit. TROLL has substituted it largely by the idea of non-disjunction (Nichttrennung). It is, however, not clear if in flower morphology he will also be able to avoid the term of fusion. We will include here under fusion cases where two primordia, usually separated, grow out together or where there is lack of complete differentiation. Seen in this way the term of "fusion" still expresses the idea that the leaf of *Bauhinia* is homologous with two leaflets.

The main arguments against coalescence are:

1. The lack of the typical vein-point of leguminous leaves on the tips of the two leaf halves.
2. The presence of a palmate nervature in the leaf halves of types *b* and *c*, which also distinguishes them from ordinary leguminous leaflets.
3. The fact that the leaf halves are not folded in the embryonal state, as leguminous leaves are.

We will see that these points indeed, though not in contradiction of fusion in general, render a fusion between ordinary leaflets less probable at first sight. In the following all available data about the leaves are arranged systematically in relation to the possibilities of "splitting" and "fusion", or other explanations.

Cross references will not be given by page number, but by referring to the subdivisions given in the initial survey of the contents of this paper.

B. COMPARATIVE MORPHOLOGY

1. *The subfamily*

As a rule *Caesalpinioideae* have paripinnate leaves. For this reason one is at first sight inclined to consider the bifoliolate leaf of *Bauhinia* as the original form. Simple or unifoliolate leaves would be strange.

2. *Monojugate relatives*

Some *Caesalpinioideae* with monojugate bifoliolate leaves show a strong likeness to type *c*. Such instances, suggesting type *c* as the primitive one, are *Cynometra cauliflora* L., *Cassia bauhinioides* Gray, *Hymenaea* species, *Trachylobium verrucosum* Oliv., *Hardwickia binata* Roxb., and *Copaifera mopane* Kirk. Of these *Trachylobium* is especially important as it has just the same differentiation in three types of joints as *Bauhinia* (cf. fig. 1). Its primary leaves show a specially striking similarity with those of *Bauhinia* as the venation is the same and even the bristle between the halves is present. The compound (monojugate) leaves of *Hardwickia binata* cannot be distinguished from the leaves of *Bauhinia* type *c* (cf. fig. 1d). In monojugate leaves (even in those of *Hardwickia binata*) the sides of the leaflets that touch in the median line are in these plants often reduced. This suggests the possibility that in *Bauhinia* only the two outer halves may have been left and that the latter may have fused in some species.

An abnormal leaf of *Hymenaea courbaril* L. from Buitenzorg was highly suggestive in this direction. It was kindly sent by Mr C. VAN WOERDEN, curator of the Botanic Garden. The two leaflets had fused with the joints and the basal parts of the blades, giving a product strongly resembling a bilobate *Bauhinia* leaf. The two main veins were united over a distance of 1—1.5 cm from the base. Originally I considered it as a weak point in this comparison that in real monojugate leaves the leaflets have only their own joints, while in *Bauhinia* the two leaflets or the two halves have their own leaf joints, but are both inserted on a common apical pulvinus. We will see however, that *Trachylobium* and *Hardwickia* form a link between these divergent structures (cf. C 1). In these relatives the monojugate condition can only be seen as a reduction of a pinnate leaf. It is not possible to consider their leaves as derived from a split *Bauhinia* type. It is to the contrary clear that *Bauhinia* is the more derivated type.

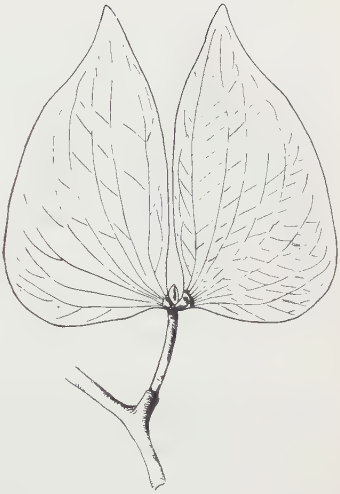

Fig. 2. Copaifera mopane, monojugate compound leaf. (after Hutchinson). In young plants I found no petioles.

3. *Imparipinnate relatives*

Bremekamp (1) pointed to *Caesalpinioideae* with imparipinnate, trifoliolate leaves, like *Krameria*. This makes type *a* and the "simple" leaves of the related genera of the *Bauhinieae* (*Cercis* and *Bandeiraea*) less exceptional and enigmatic. Speaking generally the group of the *Caesalpinioideae* is not so well defined that it is easy to say what genera are most closely allied to the Bauhinieae.

4. *Leaf or leaflet*

It is necessary to digress here on the morphology of leguminous leaves in general, because the value of the apparently simple leaves of type *a* and of the genus *Cercis* is not unequivocal. Most authors, especially Uittien (9), call them simple, probably ignoring the apical joint. Is it, however, really necessary to consider this leaf type as a reduced form, as the apical leaflet of a pinnate leaf? For many leguminous genera, like *Desmodium*, this interpretation is generally accepted and it is favoured by the presence of stipellae on top of the rhachis. It may be asked whether the presence of a double pulvinus can be considered sufficient proof for this interpretation. Velenovsky (11) (his fig. 185) already expressed doubt. Perhaps the petiole between lower and upper pulvinus is not simply homologous to the rhachis of a compound leaf. It may sometimes be a growth zone intercalated between two parts of the single pulvinus of a real, simple leaf. The question whether *Bauhinia*, *Cercis* a.o. have a leaf or a leaflet may, however, be left aside so that we may return to the main point, splitting of an originally simple part or fusion between two originally separated ones.

5. *Cercis and Bandeiraea*

If we should finally conclude that in *Bauhinia* type *a* marks the end of the developmental range, this would have unexpected consequences for two nearly related genera of the *Bauhinieae*, viz. *Cercis* and *Bandeiraea* (*Griffonia*), resp. of types *a* and a_1. Their leaves are clearly homologous with those of *Bauhinia* type *a*. Without this comparison nobody would have suspected them of being compound structures. Yet their venation (mostly palmate) and the apical pulvinus mark them as something special in the family. The leaves of *B. flammifera* are exactly like those of *Cercis*. Fries and Uittien accepted this consequence and considered the leaves of *Cercis* as fusion products.

6. *Comparison of the leaf halves with stipules and stipels*

The peculiar structure and venation of the leaf halves suggests the possibility that they might be homologous with organs other than leaves, in the first place with stipules. The description given by Troll (8) (p. 1281) of *Cassia basifolia* Vog., where two leaflike stipules are found one on each side of a bristle that represents the leaf, points to the same possibility. In *Bauhinia* a stipular nature of the leaf halves is out of question, as the leaves have two stipules at the base. These stipules too however, have very peculiar features, e.g. the occurrence of thorns in their axils (cf. Urban (10) the inequality of the two partners in some cases etc. The trichomes in their axils, described by Urban, are homologous to the colleters found in the axils of the sepals and of the cotyledons. The one that in American species is thornlike is, in those species I investigated, mostly represented by a nectar secreting thread. I first thought these threads might be identified with the prophylls of the axillary bud. In cross sections of growing-points of *B. purpurea* however, it is clear that they originate from the basal part of the stipules in their very early life. They imitate as it were the axillary buds of the leaves proper. In his "Die Pflanzenwelt" Warburg says (p. 179) that in some American species these stipular threads do not develop into thorns, but into tendrils.

7. *Comparison with other organs*

It is not necessary to confine our discussion to a comparison with the leaves of other plant species but we may compare the foliage leaf of *Bauhinia* with other organs of the same plant. I refer to Uittien's (9) attempts to find a parallel between leaf venation and inflorescence structure and even between primitivity of flower and leaf. He thinks that since the flowers of *Bauhinia* are primitive as compared with those of other *Bauhinieae*, its leaves too may be of a simpler type. It seems rather dangerous to apply this peculiar method to the flowers and leaves of the three *Bauhinia* groups. Of course it is justified to look for indications in favour of splitting or fusion in metamorphosed leaves as bracts and petals. It is curious that in none of these structures the least trace of a compound nature can be found. Never do bracts look double. The apical bristle, however, is always prominent. It is tempting but very speculative to compare the curious tendrils of some

Bauhinia species with their leaves. TROLL's figures on p. 850 show a double spiral with a rudimentary top between. Though this forms a striking analogy with the leaves there is no indication of homology. The homology of the tendrils and their bearers hides some riddles. They are compound just as the leaves possibly are. From URBAN's (10) study it is clear that not only the tendrils, but also the inflorescences are compound structures with a tendency to condensation into something apparently simple, with an arrested top rudiment and two flowers. In D 3c and D 4 comparisons even with cotyledons will present themselves.

The zig-zag build of the young stem, with the leaves in alignment with the preceding part of the axis, suggests a sympodial structure of the stem. The situation of the leaves, however, is not in accordance with this idea. The axillary buds lie between the leaf and the continuation of the stem and there are no traces of arrested main axis ends.

C. PHYSIOLOGICAL AND ECOLOGICAL DATA

At night the whole leafblade of type *b* and both leaflets of type *c* together perform a movement vertically downward. Besides this the two halves perform inter se another upward movement resulting in a folding together. This folding happens also after too strong an illumination. As in all nyctinastic movements the ecological function of these changes of position is not clear, but the folding is a constant character. In *Bauhinia* it serves the two usual "purposes": the "sleep" at night and the avoiding of too bright light at noon. The latter function is usually considered as being the primary one, though in the most primitive plant with such leaf movements (the fern *Marsilea*) the two functions already go together.

1. *Leaf movements and fusion*

Fusionists explain the folding up as a consequence of the leaf's complex nature. According to them the two original leaflets have kept their independent way of moving in their own leaf joints. However strong this argument is, it does not explain why the complex product also has a common joint (our secondary pulvinus). It pleads against fusion that in binate leaves the two "leaflets" do not perform their downward movement independently-as is the rule in leaflets. This movement happens in the common joint. Since we know that *Trachylobium* leaves possess a common joint as well as separate leaf joints, this common movement of leaflets is no longer an objection. In *Trachylobium* the leaflets of young plants move just as the leaf halves of *Bauhinia* viz. with separate joints for folding up (the leaflet joints) and moving downwards (the common joint). I think the same happens in the monojugate leaves of *Hardwickia binata* and those of *Copaifera mopane* (*Colophospermum mopane* Kirk ex Leonard).

2. *Leaf movements and splitting*

"Splitters" have more trouble to explain the movements than fusionists. According to them the tendency to fold up must be some new adaption to light factors, starting in the simple leaves, where it is not completely developed. In type *a* the folding at night is less apparent but can be seen for instance in young leaves of *B. flammifera*. These, however, still have an incision of 4 mm on a length of 95 mm.

In herbaria leaves of type *a* are found folded up more frequently than can be explained by youth only. In *B. platycalyx* Benth it is difficult to flatten the leaves entirely when preparing them for herbarium material. No actual folding up was seen in the living leaves of *B. Kockiana* and many other species with simple leaves. *Cercis* does not fold its leaves. Of course it has no explanatory value to kill the question by attributing the movement to a repetition of the unfolding movement in the sense of GOEBEL. The motile tissue at the base of the leaf halves is not an "unfolding joint" active in youth only, though an unfolding tissue may have been the starting point of the new development. According to "splitters" the incision and the final bipartition may be an expression of the tendency to facilitate the folding up. This agrees with what I saw in *B. scandens*, viz. that the deeply split leaves of young plants folded at night, but that the later ones, where the incision was not not much deeper than $\frac{1}{4}$ of the total length, remained unfolded, even when dying, (cf. E 2). This expression of a tendency should be seen in the light of the "Gestaltungstypen" of TROLL, as expressed in his "Organisation und Gestalt im Bereich der Blüte". The ecological moment has become a morphological force. In the same sense nyctinastic movements and the dividing up of the leguminous leaf into leaflets are possibly related. And this "Gestaltungskraft" may tackle the big leaflet of the type of *Cercis*, repeating the process of leaf folding by dividing it first.

3. *Morphology and habitat*

Starting from the reasoning in C, 2 it is remarkable that indeed the leaves of type *c* show the most obvious play of the leaves. In a specimen of *B. winitii* I saw the two halves assume a profile position during the whole day, entirely covering the original upper side of the leaf. This side is entirely devoid of stomata. This relates to a plant from a shadowy place in Buitenzorg, brought to a less covered place in Bandung. After some weeks all the branches died. The newly formed branches at Bandung, however, orientated their leaflets horizontally. Obviously the plant is very sensitive to light. In *B. purpurea* both sides have stomata. It is impossible to find a correlation between leaftype and ecological factors in the milieu. Many species are lianas occurring in rain forests or in thickets. Types *a* and *b* are certainly represented among them, but I think type *c* is too. Other species occur as trees in savannahs or wet forests. The two bifoliolate species I know well (*B. winitii* and *B. blancoi*) seem to prefer very exposed places as plains and shores. These two species have small leaflets but in other bifoliolate species the leaflets are very large, up to 40 cm length, e.g. in the Bornese *B. diptera* Bl.

4. *The mechanism of the movements*

The nightly movements of the leafblade as a whole make bristle and "midrib' fold themselves back in such a way that their underside touches the petiole lengthwise. The bending happens in the apical common joint. This joint mostly allows no other movement. Only in very extreme cases (when leaves had to turn 180°) a torsion or bending to the left or the right occurred in it. This movement is no repetition of the movement of the young leaf when unfolding. The movement of the two halves occurs in a plane perpendicular to the former one. The bending is executed by means of the two laminar joints (see under D, 4). The orientation movements by which the blade places itself perpendicular to the light also take place in the laminar joints. One laminar joint then moves its leaf half downward and the other upward, — the blade as a whole remaining in one plane. This illustrates how these two laminar joints can behave independently and are not active in unfolding only. All joints together illustrate a tendency to differentiation of motility into two separate directions. At the same time *Bauhinia* shows a combination of the two types of nyctinastic movement in leguminous leaves, the one being downward, the other upward. The basal (primary) joint is able to execute movements in all directions.

D. ANATOMICAL DATA

1. *The bristle*

The apical bristle might in *Cercis* and many *Bauhinia* species simply be accepted as the veinpoint (mucro) of a leaflet or a leaf. On further consideration, however, the organ is too important to be accepted as such, as will also become evident in the study of its development (E, 3). The bristle is often very large and persistent, even in "simple" leaves, where the top region seems well developed and looks regular and acute.

In the simple leaved *B. assuruana* Moric. from Brazil the long bristle gives the leaf a fantastic appearance (fig. 3). In simple leaved species like *B. bidentata* the bristle has the same sharp kneecurve that the rhachis end of a compound leaf often shows. Even in the apparently simple leaved *Bandeiraea speciosa* Wills. the bristle is abnormally long for a mere vein point. That the bristle even in "simple leaves" with a very long and narrow tip (fig. 4) is situated at the bottom of an incision is very curious. This incision in type *a* can readily be accepted by fusionists as a remnant of the deeper incision in types *b* and *c*. To consider it as a beginning of the split in type *b* is far more artificial. This argument is decidedly against the interpretation of "splitters". In some simple leaved species there is not only a tendency to fold near the base (cf. C, 2) but also near the tip. It is then difficult to flatten the top region. This feature is difficult to be explained by "splitters".

A detailed microscopic investigation of the bristle is necessary, but one can understand that on the strength of the above mentioned facts fusionists already accept it as more than a leaf tip. FRIES (2) ventured the speculation that it also contains the midrib-ends of the fused leaflets. The appearance in *Cassia basifolia* (cf. B 6) of a bristle representing the whole "Oberblatt" strengthens this opinion. For developmental data see E. One result may be discussed here beforehand. In the bifoliolate leaves of *B. binata* the bristle is in early youth externally equal to the two lateral protuberances that develop into the "leaflets". It is dorsiventral and concave as if folded and it encircles the edges of these "leaflets" like a roof (cf. fig. 7). This might be seen as proof of its nature as a leaflet. In other species too the bristle is more or less flat.

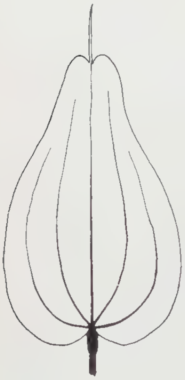

Fig. 3. Leaf of Bauhinia assuruana

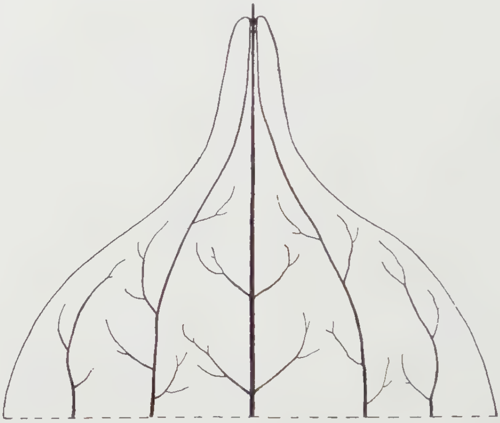

Fig. 4. Bauhinia pyrrhaneura.

When comparing *Bauhinia* leaves with compound leaves one is struck by the resemblance of the bristle with the top of the rhachis that projects between the apical pair of leaflets of a pinnate leaf. In this relation it is indifferent if the top represents only the rhachis or the rhachis with the reduced terminal leaflet. The flat rhachis end of *Copaifera* (fig. 2, 8) finds its homologon in the flat bristle of *B. binata*.

"Splitters", however, can also accept the bristle as more than just a veinpoint. According to their views it may represent the arrested top portion of the leaf proper. That in all the species investigated the bristle is provided with a vascular strand agrees with both conceptions. Figures like the one in fig. 4, where the top region of the leaf has a number of parallel veins may lead to a comparison with Acacia phyllodes. The bristle on top of the phyllodes of some Acacia species, representing the lamina proper, has also much likeness to the bristle of *Bauhinia*.

Accepting for a moment the leaf of *Bauhinia* as a phyllode it should be compared to the alate rhachis of species like *Desmodium triquetrum*, broadened laterally, not medially like in Acacia. The bristle then would be the lamina.

The difference between pleuroplastic development of the basal portion of a folded leaf and the broadening of the wings on both sides of a petiole is perhaps not so essential.

So many points, however, disagree with the nature of the *Bauhinia* leaf as a phyllode, that this idea should not be considered too seriously.

2. *The apical leaf joint*

The primary pulvinus has a normal structure and functions in the normal way. The apical pulvinus bends in only one plane, but is very active. As said before it is easily overlooked in herbarium material. TROLL (8) (p. 1025) ignored it. UITTIEN (9) (p. 406) even denied its existence.

Internally it has a very complicated structure. The vascular system induced FRIES (2) to consider the joint as a double structure, as the fusion product of two joints. On the one hand it is a fact that WATARI (12) and the many writers (BOUYGUES, COL, ACQUA, PETIT) on the subject cited by him classify the apical joints of *Cercis*, *Bauhinia* and *Bandeiraea* as abnormal joints, deviating from all other leguminous leaves. The figures of FRIES contain many more details, but are in some points not very accurate. The differentiation between types with blunt and acute leaf halves is not tenable. Even the acute ones never have a real veinpoint. On the other hand he omits in his fig. 5 the really very conspicuous bristle of *B. bidentata*. In *Cercis* joints he figured the median vascular bundle, but not in *Bauhinia*.

Now fusion in joints of leguminous leaves cannot be ruled out. I found many instances, especially in *Clitoria ternatea*. In those cases the joint parenchyma was undivided but the vascular tissue was double (cf. *Hymenaea* in B 2). In the types *b* and *c* the double structure might find an explanation in a physiological necessity in relation to the folding up of the leaf halves, as the dividing of the two bundles must happen underneath the leaf halves. It is, however, possible to use as an argument in favour of FRIES that also in "simple" leaves of type *a* the vascular tissue is doubled, even in *Cercis*.

When speaking about the midrib (D 3d) we will also find the possibility of a physiological regulation as cause of its internal structure.

In *Bixa orellana*, a totally unrelated plant, where there is also a second leaf joint underneath the blade and where a compound nature is out of question, this apical leaf joint also shows an intricate vascular structure and the midrib arises from two of its strands. The same holds true for the many joints described by FUNKE (3). He does not differentiate between unfolding joints and joints with variation movements. The unfolding joint on top of the petiole of *Hibiscus similis* has almost the same structure as the one of *Bauhinia*. On the ventral side the stele splits, as a beginning of the flattening out into the lamina.

The internal structure of the *Bauhinia* apical joint therefore may also be physiologically determined. Its dorsiventrality certainly is in accordance with its function, movement in one plane only. Since we know that in *Trachylobium* there is a special common joint, as a new formation under the pair of leaflets, the apical joint is no longer an argument contra fusion, but strongly pro.

In *Hardwickia binata* the monojugate compound leaf also has a distinct apical joint in the rhachis. Whether it is also present in *Copaifera mopane*, I dare not say. In the young plants I observed and in the herbarium material Dr de Wit furnished, there was only a short, undifferentiated, pulvinuslike rhachis. In fig. 2 (copied from Hutchinson) we see a leaf with a distinct rhachis above the basal pulvinus, without an apical pulvinus, but perhaps this has been overlooked.

3. *The venation*

a. The absence of a veinpoint in the leaf halves. The fact that the veins of the leaf half never reach the margin and never form a veinpoint, (even when both tips are acuminate) has been mentioned already. In forms like *B. winitii*, the leaf structure gives the impression of a fern leaf for this reason and also because of the round apex and the palmate venation. The two halves are therefore, up to present standards unacceptable as leguminous leaflets, least of all in type *c*, which should be the most primitive type according to fusionists.

b. The absence of a midrib in the leaf halves. In the introduction it was already pointed out, that the general lack of a midrib in the two leaf halves is not in accordance with their possible character as two leaflets. Sometimes (it is said) we find one thick vein in the halves of type *b*, but mostly and to my experience exclusively, a number of equal veins radiate from the laminar joint. We will refer to this as a palmate venation. When the condition of separated halves (in binate leaves) would be a primitive condition, we might expect that the original midrib would be visible, in some cases at least. Never, however, did I see a pinnate venation of the halves. Nor did Dr H. C. D. de Wit, who studied the taxonomy of the genus for the Flora Malesiana. Even the leaflets of *B. diptera*, which are rather narrow and have a length of 40 cm, are palmate.

c. Palmate venation as a secundary regulation. If most points under *a* and *b* speak against the nature of the two halves as leaflets, it must be said that the palmate venation, especially in leaves of the simple type is just as little in accordance with the nature of the whole as one leguminous leaflet. Instances of leguminous plants with multinerved leaflets, like *Liparia sphaerica*, are very rare. *Cercis* always had an isolated position in this respect. The venation in leaves of type *a* is often the same as in *B. purpurea*, as may be seen in the palmate *B. bidentata*. Such leaves are almost identical with those of *Cercis*. The appearance of many collateral veins in the unquestionably true leaflets of *Copaifera mopane* Kirk (fig. 2) of a tribe very near to the *Bauhinieae* makes the situation more intricate. In this monojugate species the two leaflets have the same venation as the leaf halves of *B. purpurea* c.s. and the whole leaf is a close approach to the structure of *B. winitii*, and of *Trachylobium* seedlings which will be discussed below. Even in a bifoliolate *Cassia* species, *C. basifolia* Vog. the same has happened. (cf. E 2). In other species of *Copaifera*, including some with monojugate leaves, the leaflets have a distinct midrib with side veins. The same holds true for a different monojugate *Cassia*, *C. bauhinioides* Gray.

In an Indian *Hardwickia* species (very close to *Copaifera*) the leaflets have also acquired a multinerved condition as a secundary phenomenon. *Hardwickia pinnata* Roxb. has pinnate leaves with alternating leaflets that are pinnatinerved. The two uppermost leaflets both show a tendency to assume a terminal condition. In *H. binata* Roxb. only this apical pair is left. It is curious that the leaflets have become multinerved as in *Copaifera mopane*. The primary leaves of seedlings already show this condition. The palmate venation in this plant is not yet complete. In many leaves the innermost vein still shows traces of being the primary midrib, by having stronger side veins and by reaching the margin in a shallow incision. The similarity between the leaves of *Bauhinia binata* and the pair of leaves of the nearly related *Copaifera mopane* and *Hardwickia binata* now becomes a strong argument in favour of fusion. Perhaps the multinerved condition is a prelude to fusion or non-disjunction of the two leaflets.

In some simple leaved *Bauhinia* and *Bandeiraea* species (types *a*) a predominant midrib is visible, but this too may be a secondary transformation. Often the midrib is accompanied by two strong nerves, originating from the base. This triplinerved leaf also does not make the impression of a primitive condition and is considered as proof of coalescence by fusionists. The most perfect examples of pinnate dicotyledonous venation are found in the simple leaves of other *Bauhinieae*, e.g. in *Bandeiraea tenuiflora* Benth (c.f. fig. 1, a_1). **Fries** c.s. interpretes leaves of this type as the results of a convergent development after fusion.

As said before, venation may be regarded as more physiologically than morphologically determined. "Splitters" may use this to argue that the widening of the leaf to the type of *Cercis* (and *B. bidentata*) might have induced a pleuriplastic development of basal collateral veins, this in order to save the *Cercis* leaf as a primitive structure. Surely such an increase of veins may have happened in types *b* and *c*. The pleuroplastic development can be followed by the number of collateral veins in each half. It increases from the first to the later leaves of a seedling. In *B. purpurea* I made the following counts, in which ½ means a vein that was visible as a thickening of the margin, but was still included in it: 1st. leaf (cataphyll) 1, 1½ or 2; 2nd. leaf 1½, 2 or 3; 3rd, 4th and 5th. leaf 3; 6th and 7th. 3 or 4, and the adult large leaves 5.

The venation of the leaf halves usually makes a primitive impression as if the lamina were not a well structured foliage leaf but a secundarily stretched outgrowth of some kind. Such a venation with a varying number of collateral veins can be expected in leaf sheats, outgrown stipules and in leaves like those of *Plantago*, that have a more or less phyllodine character. We found, however, the same type of venation in the *Cassia*, *Hardwickia* and *Copaifera* species, mentioned above, where the leaflets are not broader than in other species with pinnate venation.

I must remark that in many leguminous plants (e.g. *Sesbania*) where the ordinary leaflets have a pinnate venation and a vein point, the primary leaves have a more primitive venation with some collateral veins along the midrib and a median vein that does not run through to the margin and has no vein point. I even dare say the leaf halves of leaves of most *Bauhinia's* look like regressions to cotyledons.

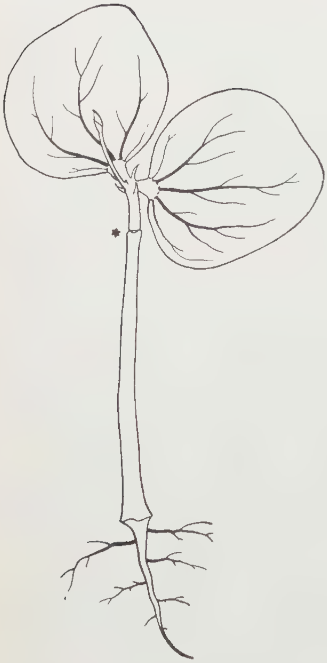

Fig. 5. Trachylobium verrucosum. Seedling with one primary leaf, complete with rhachis tip and stipulae. Scar of fallen cotyledones at the place of the asterisk.

The process of cotylisation seems to occur especially in plants with binate leaves, e.g. *Copaifera*, *Hardwickia* and *Cassia* species. In some of them the process is extremely evident in the queer, giant primary leaves. In *Trachylobium verrucosum* the two primary leaflets imitate cotyledons in an amazing way (fig. 5). They are rather thick, round, without mucro and palmate in contrast to foliage leaves. LUBBOCK (5) gave a figure of the almost identical seedlings of *Hymenaea courbaril* L. (his fig. 305), also with binate leaves. The text accompanying this figure speaks of two simple, opposite, primary leaves. On p. 398, however, he nearly gives the correct explanation: a sessile binate leaf with leaflets having the appearance of simple opposite leaves. Besides the cotyledonoid appearance of the leaflets the long lasting inhibition of growth of the stem above this leaf makes the epicotyl an exact repetition of the hypocotyl plus cotyledons. I do not know whether there is also a correlation between the monojugate and the multinerved condition in other families, e.g. *Simarubaceae* and *Zygophyllaceae*, but amongst *Leguminosae* the common *Lathyrus* is another instance of it.

The arguments under *a* and *b*, which first served against the interpretation of the leaf halves as leaflets, viz. lack of a veinpoint, lack of a midrib and presence of palmate venation, lose their value now that we found all three phenomena in real leaflets as components of one physiological syndrome. Probably it also includes nonfolding in the bud (cf. C, 1) and probably the opposite position of so many primary leaves is its first symptom.

With reference to the modern distrust about the possibility of fusion of leaves, I should like to point to the well-known cases were the two cotyledons of *Leguminosae* have grown together. (*Astragalus* and

Hedysarum). Seeing this the fusion of two cotyledonoid leaves is not so improbable.

d. The midrib. According to the "splitters" the midrib when poorly developed may be seen as affected by the apical growth inhibition. It seems uncertain if this is a sufficient explanation for its internal reduction in bilobate species like *B. purpurea*. In other plants with pleuroplastic developement, like *Cercis*, *Ipomoea pes-caprae* and *Lourea* the midrib is shortened indeed but it sends out many side veins and is still physiologically important. In *Bauhinia purpurea*, however, the midrib is, though seemingly thick, entirely unimportant. It has no side veins or almost none and contains but few and thin veins. VELENOVSKY already noted this. When a leaf is made to suck up a solution of methylene blue, the dye soon becomes visible in the nerves as a thick line extending to the top in the leaf halves, but in the midrib it shows as a thin line in the lower part only. These data have from a morphological point of view restricted value. The reduction may have no morphological background at all, but may be a physiological regulation as said under *c*. It may also be a necessary consequence of the mighty tendency toward folding up. The lack of side veins facilitates folding along the midrib. This in its turn makes lateral veins necessary as a compensation.

On the other hand the fact that in simple leaves (type *a*) the midrib is well developed is not necessarily a proof for the primitivity of this type either. This too may be a secundary regulation. As we saw venation is nowadays often considered as less important in morphological questions. Of course a peculiar type of venation to which no

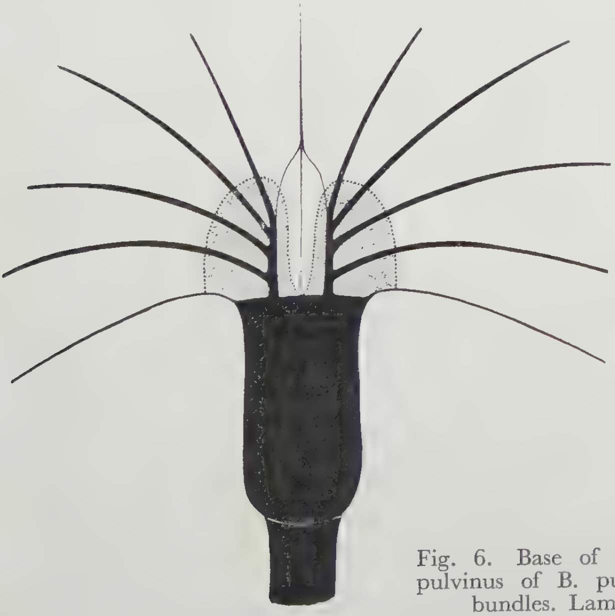

Fig. 6. Base of lamina and secundary pulvinus of B. purpurea with vascular bundles. Laminar joints dotted.

physiological significance can be assigned, will always remain a valuable indication for the morphologist.

For the time being we will have to admit that the origin of woody elements in the midrib of *B. purpurea* seems to point to a compound and derivative nature. The woodvessels are partly a continuation of a small unpaired median bundle from the apical joint that is not always easily detected. The main contribution comes from right and left as the end of the two bundles that branch into lateral nerves of the leaf halves (cf. fig. 6).

I may refer here to the detailed figures that WATARI (12) gave of the vascular strands in the petiole tips of *Bauhinia* and *Cercis* (his figures 13A and 15M). For *Cercis chinensis* he figures a midrib out of one single strand in the petiole. Fusionists might consider the contributing bundles from the right and the left as the remnants of the main veins of the fused leaflets. It is most interesting that in *Cercis siliquastrum* too the "midrib" in spite of its seeming simplicity arises in a complicated way out of three separate bundles in the apical joint. The median small bundle cannot be detected here. It is as yet uncertain whether any morphological deductions can be based on this fact. In the apical joint of *Bixa* the midrib also originates from bundles from left and right, as we described under D, 2. In the figures of WATARI we see that in many leguminous plants (e.g. *Trifolium*, *Lupinus*) the midrib of true leaflets also arises by the fusion of vessels from different vascular strands in the petiole.

4. *The laminar motor zones*

Cushions of motile parenchyma cover the converging bases of the digitate veins in both halves of the lamina base near the points of contact with the petiole. They are best visible on the upper side of the leaf. That these cushions, referred to as the laminar joints, regulate the motions of the leaf halves, follows from simple experiments where the cushion either on the upper side or on the lower side is cut away. In this way leaves can be made to close and open instantaneously. In his "Die Pflanzenwelt" (vol. II, 1921, p. 178) WARBURG says that none of the halves has joints and he uses this incorrecte statement to deny their nature as leaflets. Simple leaves also show these cushions (cf. C, 2). They are even visible to some degree in *Cercis*, though no motions were ever observed by me. Many *Bauhinia* species (very clearly *B. picta*, *variegata* and *monandra*) show just the same motile tissue at the base of the cotyledons. The converging veins also remain separate inside this "joint". It is undivided and causes no folding, only a movement up and down. In *B. tonningii* cotyledons have some kind of a petiole. The daily movements are not executed by means of a motor zone at its base but by a thick cushion that covers the base of the lamina and the top of the petiole. When compared to the adult leaf this cushion looks as if homologous to the laminar joints and apical pulvinus combined. In many species of *Bauhinia* the sepals have the same kind of mobile tissues at their bases. By means of this they bend back when the flower opens. Even the stipules may show the same phenomenon. According to "splitters" the laminar joints must be new formations, already present in *Cercis*, where they serve no purpose in the full grown leaf. Under C, 2 we already saw that the cushions in *Cercis* and the like might be considered as derived from "unfolding joints"—only there is no trace of such tissues in any young leguminous leaf. To fusionists the laminar joints are homologous with the leaflet joints or parts thereof. This sounds plausible, the more so as the common (apical) joint of the petiole can be recognised as already present in *Trachylobium* and *Hardwickia*.

When the leaf halves are phyllode-like outgrowths or stipels these joints are also new, though there is a parallel in stipular joints.

E. The Developmental History

1. *The vernation*

In the introduction the fact that leaves of type *a* and *b* are in youth folded, just like ordinary leguminous leaves, was mentioned already.

If the leaf halves were originally leaflets one could demand that they should be folded separately as most leguminous leaflets are. Even in the separate "leaflets" of type *c*, however, I saw no trace of this folding. The vernation of type *c* remains to be investigated more thoroughly. Perhaps this argument of the "splitters" looses much of its value when fusionists bring forward the argument that the leaf halves are possibly not complete, but are half leaflets. Fries already inclines to this idea (see D, 1). The leaflets of the monojugate *Cynometra cauliflora* might here be used as a model. They are strongly asymmetrical by a reduction of the sides touching each other (cf. B, 2). In young leaves of adult plants the narrow inner half is bent somewhat, but is not folded against the outer half. In seedlings they are folded in the bud. It is important that the leaflets of *Copaifera mopane*, which have palmate venation like the leaf halves of most *Bauhinia*'s are also not folded in the bud (fig. 8). Neither are those of *Pithecolobium dulce* (also asymmetrical and monojugate). Those of adult plants of *Trachylobium*, *Hymenaea stilbocarpa* Hayne and *H. courbaril* L. are folded when young, but their primary leaves are not.

2. *The leaves of the young plant*

Velenovsky already was astonished that in *Cercis*, the leaf of which he considered as a double thing, the young seedling does not show the least trace of the supposed double nature of the leaves. The same holds true for *Bauhinia* of which I studied the germination in a great number of species, kindly sent by the curators of the Singapore and Buitenzorg Botanic Gardens. Unfortunately seeds of types *a* and *c* were not available, but we already know from Lubbock (5) (p. 465) that in the binate *B. carronii* F. Muell. the primary leaves of seedlings are also bifoliolate. The only result of interest of my cultures was procured by the teratological deviations discussed under F. Mostly the first leaves are large and of the adult type. In some species (*B. violacea*, *rosea*, *purpurea*) they are preceded by small cataphylls, not fundamentally different from the adult type. *B. scandens* L. var. *Horsfieldii* Miq. ex Prain (the well-known "monkey rope") has the leaves split deeply in young plants, whereas those of full grown lianas are sub-entire with the incision reaching not more than 5 mm on a total length of 70 mm. I will not venture to draw conclusions from this curious fact, but it is not favorable to simple splitting. In *B. flammifera* this difference is also present, though not as marked. The lack of deviating leaves on seedlings of *Bauhinia* and *Cercis* is the more impressive as in other *Caesalpinioideae* seedlings show leaves of a special type. The study of their homologies (D, 3c), however, shed no light on the *Bauhinia* problem and made it even more intricate. In one species of monojugate *Caesalpinoideae* with palmate leaflets (*Copaifera*) the first leaves were also palmate. In some monojugate species with pinnate adult leaves the first leaves were palmate (*Hymenaea*, *Trachylobium*). The palmate leaflets of *Cassia basiflora* figured by GOEBEL (4) (fig. 1357) and by GLUCK are also from primary leaves. In normal leaves the lamina has disappeared (cf. B, 6). The results of *Hymenaea* and *Trachylobium* should not be explained in the sense of the biogenic law, as proving that palmate venation is more primitive than pinnate venation. The first leaf is simply more cotyledonoid.

3. *The development of the leaf*

First I will consider the best known species, *B. purpurea*, of type *b*. "Splitters" should expect a more simple outline in proportion to the leaf being younger. Fusionists should expect a more pronounced double structure. Both expect a median point, either leaf tip or rhachis tip. The fact is, that in the first stages the bristle is in proportion astonishingly large and that the two halves are small, but well differentiated. (cf. fig. 7d, e). This might still be explained as a leaftip with pleuroplastic development underneath, though the median bristle is improbably large for just a leaftip at this stage. In the simple leaved *B. bidentata* (fig. 7c) the initial stages have the sideward wings less pronounced. The knee in the bristle is a striking feature, somewhat uncommon in a leaftip. The whole reminds one strongly of the differentiation between leaflamina-rest and the broadened petiole in *Acacia* species with phyllodes (cf. TROLL (8) (fig. 995). More illuminating is the leafprimordium in the double leaved *B. binata* (cf. fig. 7a, b). It cannot be distinguished from the primordium of a monojugate compound leaf e.g. of *Copaifera mopane*, where the top of the rhachis is a flat protuberance. It consists of three more or less equal segments and certainly does not give the impression of a simple leaf with terminal inhibition. The median segment, the bristle, looks more like a leaflet itself accompanied by other leaflets or stipels. Of course it may also be homologous to the flat rhachis top seen in *Copaifera* a.o. genera (For the bud position of halves cf. E 1).

Serial sections of growing points reveal the distribution of meristematic tissue in young leaf primordia of *Bauhinia* species. In a binate species like *B. binata* the common base and the central lobe (the bristle) were found to lose their meristematic character very early (fig. 9). What later on develops as the "leaflets" arises as wings from meristematic tissue on both sides of the groove in the common base. In a bilobate species like *B. purpurea* the difference in cell diameter and protoplasma density between the common base (the later midrib)

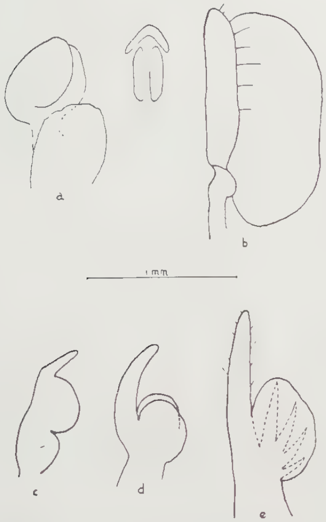

Fig. 7. Young leaves of different Bauhinia species, all at the same scale.
a. B. binata very young with stipule.
b. B. binata somewhat older, without the basal part. Cross section in between.
c. B. bidentata.
d. and *e.* B. purpurea.

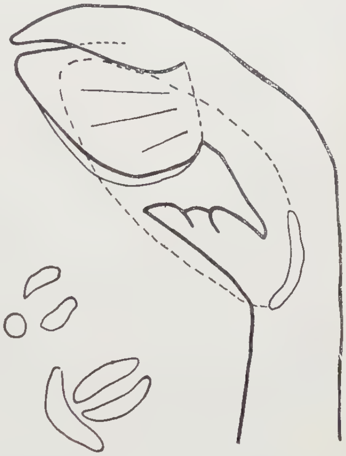

Fig. 8. Copaifera mopane. Growing point of young seedling, above the primary leaf. Stipule of oldest leaf cut away, scar and outline indicated. Cross sections through this leaf at different levels.

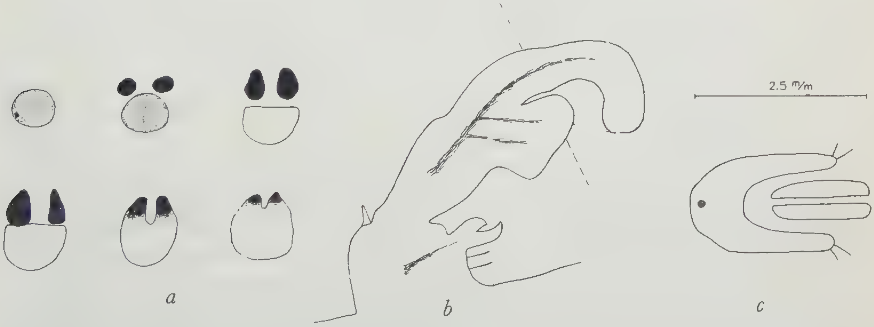

Fig. 9. Sections through young leaves of B. binata, all at the same scale.
a. Very young. Cross sections at different levels from top (upper left) to base (lower right). The more a tissue is meristematic the darker it is tinged. Bristle not yet concave.
b. Longitudinal section almost median, with axillar bud, axillar colleters and part of stipule.
c. Slightly older. Cross section along the dotted line in *b.*

and the lateral outgrowths is less marked. In a simple leaved species like *B. kockiana* and *B. cordifolia* this common base remains entirely meristematic so that it is understood that it can stretch lengthwise together with the "wings" (cf. fig. 10).

This is not just describing the difference between types *a*, *b*, *c* in other words. Combined with what we found about the shapes of very young leaves, with the idea of cotylisation in the leaf primordia (which makes them broader than is usual in *Leguminosae*), it offers a possibility to fusionists to explain the simple leaves of type *a* as double structures. Parts of the broad primordia with the palmate veins do not differentiate into pulvinus and lamina, but grow out together with the meristematic rhachis part, as indicated in fig. 10.

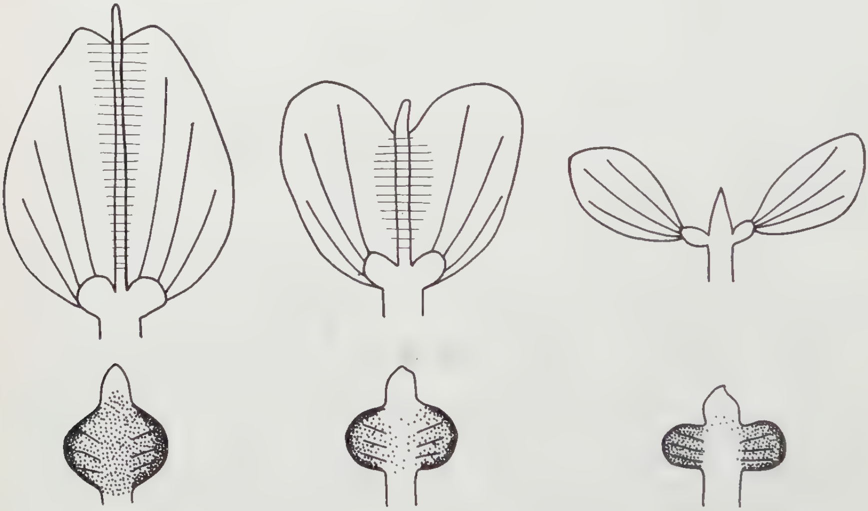

Fig. 10. Fusion as a consequence of broad insertion and distribution of meristematic zones. Meristematic tissue indicated by dots. Intercalary stretched zone indicated by stripes.

F. TERATOLOGICA

1. *Foliar asymmetry*

A considerable percentage of the first leaves of *B. variegata* are asymmetrical. This unequal development can lead to disharmony in the common midrib zone, so that the larger half forms bulges and becomes distorted. This disharmony shows the two halves as more independent than leaf halves usually are. In sprouts that arise from the axils of the cotyledons after removal of the plumula the foliar asymmetry is very frequent in other species too. In *B. acuminata* 75 % of the first two leaves are asymmetrical. In *B. picta* and some other species the asymmetry is still evident in later leaves. They sometimes tear up spontaneously. In *B. tonningii* (bilobate) I found the case of asymmetry figured in fig. 11. On one side lamina, petiole and stipule were well differentiated, on the other not at all. In other cases the first named side was also so much larger that it occupied a terminal position with the midrib horizontally orientated. The absence of teratological and juvenile forms demonstrating the double character of the apparently simple leaf pleads against fusion. The absence of abnormalities where the bristle grows out into a lamina pleads against splitting or terminal inhibition as the cause of the peculiar shape.

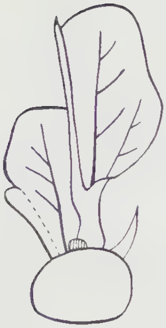

Fig. 11. Abnormal (assymmetrical) leaf of B. tonningii. – Axillar bud striped.

2. *Abnormal position of the bristle*

Seedlings of *B. variegata* from the Buitenzorg Gardens showed the curious abnormality that the bristle was not terminal but placed halfway the length of the under surface of the leaf, like the stalk in a peltate leafbase. Out of five seedlings the peltate tip was found in 6 of the first and second leaves. This de monstrates that the leafblade is independent from the bristle and that the bristle is not just the leaftip.

DISCUSSION

The author has no pretention of having solved completely the riddle of *Bauhinia*, one of the most difficult of botanical morphology. Many new arguments, however, have been discovered and many old ones have lost their value.

Combining all data pro and contra fusion or splitting the following can be said. (All data not outspokenly positive in one direction of another have been omitted, also as neutralising each other).

Definitely against splitting are the points: B, 1; B, 2; B, 3c.

In a negative way are not against splitting: B 3, B 7, E 2.

More or less pro fusion are: B, 1; B, 2; D, 1; D, 3c; D, 4.

In this way we reach, in a democratic though not exactly scientific way, a vote of: Fusion 8, splitting 3. The points B, 2 and B, 3c should get extra-value, augmenting the majority of the fusion-concept.

For the phyllode, or stipellae concept but superficial support could be found.

Though the patient detective work gave much satisfaction, the results obtained are of course not entirely satisfactory. Perhaps new methods will give a more unanimous decision. Botanists here feel the lack of the support given to zoölogists by the study of embryology.

Some more general considerations can perhaps strengthen the majority vote.

Is it possible to judge about fusion or splitting independently from the details and considering them as a whole? Is it, speaking generally, more plausible to accept the sequence *a*, *b*, *c* than the sequence *c*, *b*, *a*? (No other series are considered possible).

What might be the developmental tendencies, ecological moments or structural relations behind both sequences?

What is most likely to have happened, knowing the family?

The sequence of fig. 1, viz. a_1, a, b, c, d, e represents the splitting concept. In terms it might be described as follows: Terminal leaflet or simple leaf obtaining a secund pulvinus, cotylisation (rounding off near the tip, broadening, appearance of collateral veins), reduction of the midrib, tendency to fold as in the bud (facilitated by the palmate venation and the disappearance of sideveins from the midrib), deepening of the apical incision by inhibition of topgrowth, finally leading to the bifoliolate condition.

What is improbable here? The beginning and the end!

The appearance of an apical incision, of laminar motor zones and a long bristle in the beginning of the range (a_1) is strange.

In a way this sequence is a consequence of the tendency amongst *Leguminosae* to split up the leaf or of repeating itself. Only it is a somewhat strange detour to obtain by this convergence a condition already present in closely related genera and obtained there in a simple and usual way.

According to this concept the absence of a midrib in the free leaf halves would mean that the end of the development into two separate leaflets has not yet been attained. The difference with the leaflets of *Trachylobium* should be essential, although the plants are in other respects closely related.

Now let us consider the opposite sequence, *d, e, c, b, a*, a_1. In terms this might be described as: a monojugate compound leaf (nothing special in the subfamily), with an extra joint in the top of the rhachis, both leaflets with multiplication of the veins and with a broader insertion, which leads to the unification of their primordia or common stretching of parts thereof, which finally gives one lamina. Ultimately this lamina changes its parallel venation back into the normal dicotyl venation and loses most traces of its origin.

What is improbable here? At first sight it seemed strange, that no species of type *c* has the original midrib of the leaflet, but assuming that cotylisation occurred before the fusion this objection loses its value.

That type a_1 is a convergence to the normal shape of a leaflet is strange, but is acceptible as it agrees with some peculiar features, that now prove to be relics.

The above considerations strengthen the conception of fusion in Bauhinia.

Special thanks are due to Prof. Dr C. E. B. Bremekamp and Dr H. C. D. de Wit for their valuable criticism.

REFERENCES

1. Bremekamp, C. E. B., Het Bauhinia Blad. De Trop. Natuur 29, 1940, p. 71.
2. Fries, R. E., Zur Kenntniss der Blattmorphologie der Bauhinien, Arkiv. f. Botanik Bd. no. 10, (1909).
3. Funke, G. L., On the biology and anatomy of some tropical leaf joints, Ann. Jard. Bot. Buitenzorg 40 & 41, (1929—1931).
4. Goebel, K., Organographie der Pflanzen, 2nd ed. (1922).

5. LUBBOCK, J., On Seedlings, London, (1892).
6. PIJL, L. VAN DER, Het blad van Bauhinia. De Trop. Natuur, 28, p. 123, (1939).
7. PIJL, L. VAN DER, Het Bauhinia blad. De Trop. Natuur, 29, p. 71, (1940).
8. TROLL, W., Vergleichende Morphologie der höheren Pflanzen. Berlin, (1935—1938).
9. UITTIEN, H., Über den Zusammenhang zwischen Blattnervatur und Sprossverzweigung. Rec. Trav. Bot. Neerl. 25. p. 390, (1928).
10. URBAN, I., Morphologie der Gattung Bauhinia. Ber. D. Bot. Ges. 3, p. 81, (1885).
11. VELENOVSKY, J., Vergleichende Morphologie der Pflanzen. Prag, (1907).
12. WATARI, S., Anatomical studies on some leguminous leaves with special reference to vascular system in petioles and rhachises. Jl. Fac. Sci. Tokyo, Sect III, vol. IV, p. 225, (1933).

OBSERVATIONS SUR LE ROSMARINETO-LITHOSPERMETUM SCHOENETOSUM DU BAS-LANGUEDOC

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INTRODUCTION

Sur les terrains marneux du Bas-Languedoc le *Rosmarineto-Lithospermetum* recouvre de vastes étendues et constitue la majeure partie de la "garigue à Romarin", contrastant nettement avec la garigue des terrains jurassiques à sous-sol plus perméable.

J. BRAUN—BLANQUET a donné un premier aperçu de l'association en 1924. En 1936 Mme. G. BRAUN-BLANQUET en a donné une description plus détaillée et a distingué les sous-associations *Rosmarineto-Lithospermetum ericetosum, dolomiticum, helianthemetosum, atractylidetosum* et *pinetosum.*

Plus tard une sous-association *schoenetosum*, caractérisée par l'abondance de *Schoenus nigricans*, a été distinguée par J. BRAUN-BLANQUET (publication sous presse).

Au printemps de 1951, lors d'un séjour à la Station Internationale de Géobotanique Méditerranéenne et Alpine à Montpellier, nous avons eu l'occasion de collaborer aux recherches sur le *Rosmarineto-Lithospermetum* entreprises par la Station. La sous-association *schoenetosum* a été le sujet principal de nos recherches.

Notre séjour a été de trop courte durée pour permettre une étude approfondie. Néanmoins il nous semble utile de fixer les observations qui ont été faites.

Dans les chapitres qui suivent nous examinerons quelques-uns des aspects du *Rosmarineto-Lithospermetum schoenetosum.*

1. STRUCTURE ET COMPOSITION FLORISTIQUE

D'une manière générale le *Rosmarineto-Lithospermetum* est un groupement plus ou moins ouvert. Certaines espèces — surtout les sous-arbrisseaux — y ont tendance à se grouper en îlots.

Ce qui est vrai pour l'association l'est encore davantage pour la sous-association *schoenetosum*. Dans le *Rosmarineto-Lithospermetum* en général c'est surtout *Rosmarinus officinalis*, qui semble contribuer à la formation des îlots par le microclimat plus favorable aux plantules à l'ombre des buissons. Dans la sous-association *schoenetosum* c'est plutôt *Schoenus nigricans*, qui est l'édificateur des îlots.

Dans ces stations le centre des touffes de *Schoenus nigricans* meurt très souvent, tandis que la périphérie s'accroit. Il en résulte, que les touffes de *Schoenus* ressemblent fréquemment à des nids d'oiseau. Plus tard la périphérie en s'accroissant se fragmente en arcs. Ce développement est illustré par la figure No. 1.

Ces nids et ces arcs constituent un bon rempart contre le fort remaniement du sol, qui règne en général dans ce type de végétation. Il semble, que beaucoup de plantules dépendent de cette protection, surtout celles des sous-arbrisseaux. (Voir chapitre No. 2).

C'est probablement la raison pour laquelle les îlots formés par *Rosmarinus officinalis*, *Erica multiflora*, *Juniperus oxycedrus*, *Genista scorpius*, *Buxus sempervirens* et *Phillyrea angustifolia* se rencontrent pour la plupart derrière les remparts du *Schoenus*. Quelques autres espèces sensibles au ruissellement se réfugient dans ces îlots: *Lavandula latifolia*, *Genista Jordani*, *Staehelina dubia*, *Teucrium polium*, *Bupleurum rigidum*, *Coronilla minima*, *Asperula cynanchica*, *Chlora perfoliata*, *Ophrys araneifera* et *Coris monspeliensis*.

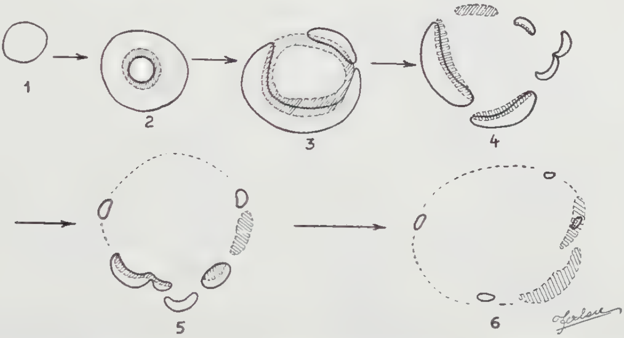

Fig. 1. Évolution des touffes de *Schoenus nigricans* dans le *Rosmarineto-Lithospermetum schoenetosum*. En blanc la touffe vivante, hachée la zone nécrotique.

Les espaces ouverts ou à recouvrement très faible, où le sol est remanié par les pluies et craquelé par la sécheresse, sont très souvent recouverts d'une carapace de cailloutis. Quelques espèces peuvent y germer et s'y maintenir sans la protection offerte soit par *Schoenus nigricans* soit par certains sous-arbrisseaux. Ce sont surtout *Fumana ericoides*, *Carex humilis*, *Stipa juncea*, *Koeleria vallesiana*, *Festuca duriuscula*, *Andropogon gryllus*, *Thymus angustifolius*, *Euphorbia nicaeensis*, *Leontodon Villarsii*, *Linum campanulatum*, *Helianthemum canum*, *H. italicum* et *H. hirtum*. — Quant à *Aphyllanthes monspeliensis*, *Lithospermum fruticosum*, *Globularia Linnaei* et *Gl. Willkommi*, ils se trouvent tantôt parmi les buissons, tantôt en dehors. *Tortella inclinata* pousse sur le sol nu, mais préfère l'abri des touffes de *Schoenus*.

Si le sol n'est plus enlevé par le ruissellement *Carex glauca* s'installe dans les espaces entre les îlots et parfois apparaissent de jeunes plantes de *Quercus coccifera* et de *Pinus halepensis*. C'est le début de la régénération du tapis végétal.

La figure No. 2 donne un exemple d'un "nid" encore à peu près intact. La figure No. 3 représente un "arc" avec les plantes, qui ont cherché sa protection.

A côté de la composition floristique, la structure en "nids" et "arcs" est, à notre avis, un caractère important de ce groupement. Cette structure ne ressort pas du tableau de relevés, ces derniers ne l'exprimant guère.

C'est pourquoi il nous semble utile, que tout relevé soit accompagné non seulement des données écologiques usuelles, mais aussi d'une courte note sur sa structure, surtout si une telle structure semble

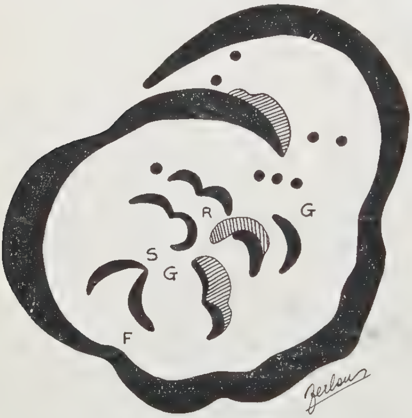

Fig. 2. Touffe en anneau ("nid") de *Schoenus nigricans*. Diamètre 80 cm. (Grabels15. 4. 1950)

■ Schoenus nigricans
▥ Carex humilis et Koeleria vallesiana.
□ Erica multiflora
░ Rosmarinus officinalis
✦ Globularia Linnaei
S Staehelina dubia
L Lavandula latifolia
C Coris monspeliensis
● Buxus sempervirens
G Genista scorpius
F Fumana ericoides
R Rosmarinus officinalis
→ Direction de l'érosion

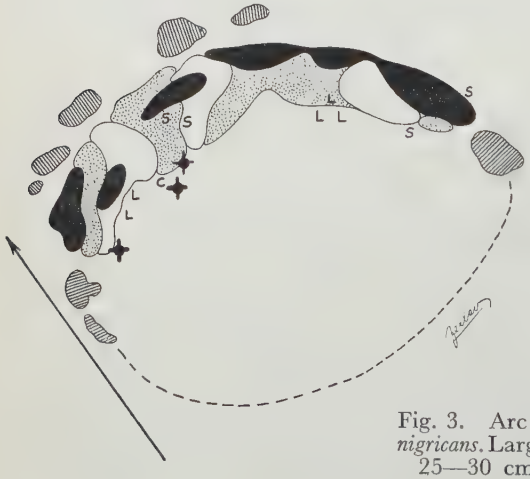

Fig. 3. Arc dérivé d'une touffe de *Schoenus nigricans*. Largeur de l'arc: 130 cm, épaisseur: 25—30 cm. (Fontfroide 8. 10. 1950).

particulière au groupement végétal étudié. Elle aidera à constater qu'il s'agit bien du groupement en question.

Un relevé ne fut incorporé dans notre tableau qu'après avoir vérifié qu'il avait bien la structure typique.

2. Distribution des plantules

Pour étudier l'évolution du *Rosmarineto-Lithospermetum schoenetosum* Ferlan et Poore ont effectué des recensements de plantules. Bientôt il apparut que les résultats étaient peu significatifs si on choisissait les surfaces au hasard dans la végétation. Par contre, si on considérait les "nids" et les "arcs" de *Schoenus* d'une part, les espaces ouverts de l'autre, les résultats confirmaient quantitativement, ce qui a été dit sur la structure dans le chapitre précédent.

À l'intérieur des touffes de *Schoenus* les plantules étaient en général à la fois plus nombreuses et plus variées en espèces, certaines d'entre elles, déjà énumerées ci-dessus, étant rares à l'extérieur.

	à l'intérieur des touffes de Schoenus	sur limon colluvial	sur sol couvert de cailloux
Erica multiflora	4% (0–2) 5	—	—
Rosmarinus officinalis . . .	+ (0–1) 9	—	—
Asperula cynanchica	+ (0–1) 1	—	—
Coronilla minima	+ (0–1) 0	—	—
Genista Jordani	1% (0–1) 0	—	—
Helianthemum canum . . .	+ (0–1) 0	—	—
Avena bromoides	+ (0–1) 0	—	—
Rhamnus alaternus.	+ (0–1) 0	—	—
Quercus coccifera	+ (0–1) 1	—	—
Phillyrea angustifolia	— — 1	—	—
Staehelina dubia.	+ (0–1) 0	—	—
Schoenus nigricans.	70% (3–5) 3	— — 1	—
Aphyllanthes monspeliensis .	3% (0–2) 0	+ (0–1) 1	—
Bromus erectus	2% (0–1) 0	+ (0–1) 0	—
Lavandula latifolia	+ (0–1) 1	+ (0–1) 0	—
Trinia glauca	— — 1	+ (0–1) 0	—
Carex humilis	2% (0–2) 0	—	2% (0–2) 0
Globularia Linnaei	3% (0–2) 3	+ (0–1) 0	+ (0–1) 0
Fumana ericoides	2% (0–2) 4	+ (0–1) 0	1% (0–1) 6
Carex glauca	1% (0–1) 0	+ (0–1) 0	1% (0–1) 0
Thymus angustifolius. . . .	+ (0–1) 1	3% (0–2) 0	+ (0–1) 0
Stipa juncea	8% (0–4) 0	4% (0–2) 0	1% (0–2) 0
Festuca duriuscula	—	2% (0–1) 0	2% (0–1) 0
Helianthemum hirtum . . .	—	4% (1–2) 17	1% (0–1) 17
Brachypodium ramosum . .	—	—	+ (0–1) 0
Koeleria vallesiana	—	1% (0–1) 0	—
Muscari neglectum	—	+ (0–1) 0	—

Les pourcentages de moins de 1 % sont indiqués par un +.

Nous reproduisons seulement un exemple de Poore, provenant de la proximité du relevé N. 40 (voir tableau) à Bel Air. (Date 22.4.1951. Terrain un peu ondoyant près d'une ligne de partage des eaux. Accumulation de limon colluvial alternant avec érosion.)

Dans chaque biotope dix carrés de 900 cm^2 ont été examinés. Le premier chiffre indique le recouvrement moyen des individus adultes (entre parenthèses le plus bas et le plus haut recouvrement selon l'échelle de HULT—SERNANDER; voir BRAUN-BLANQUET 1928). Le dernier chiffre indique le nombre de plantules dans les dix carrés.

3. LE SOL

Le régime du *Rosmarineto-Lithospermetum schoenetosum* semble avoir la caractéristique suivante:

Saturation en eau du sol pendant les grandes pluies. Puis diminution plus lente de l'humidité que dans les autres sous-associations du *Rosmarineto-Lithospermetum*. Enfin dessiccation au cours de la saison chaude et sèche.

D'après ce que nous avons pu observer la saturation ne persiste pas longtemps après les grandes pluies du printemps, le sol ne restant humide que jusqu'au mois de mai environ. Comme le printemps de 1951 était anormalement froid et humide nos observations ne sont pas concluantes.

Il y a une différence sensible avec le régime de l'*Inuleto-Schoenetum* (BRAUN-BLANQUET 1924), qui s'étale au pied des collines et dans les bas-fonds des ravins d'érosion. Ici la terre fine colluviale est alimentée par les suintements des pentes environnantes, de sorte que le sol reste longtemps saturé d'eau après les pluies. L'aération du sol y est très déficiente (BRAUN-BLANQUET 1924, MOLINIER 1935 p. 161).

Dans l'*Inuleto-Schoenetum* le *Schoenus nigricans* se comporte en général d'une manière très différente: Il forme une pelouse de petites touffes basses. Il est accompagné de *Molinia coerulea, Carex glauca, Inula tuberosa, I. viscosa, Globularia Linnaei* etc. Un réseau dense de racines de *Schoenus nigricans* parcourt les couches supérieures du sol. Il semble que les circonstances favorisent la germination de *Schoenus*, qui montre toutefois une vitalité réduite du fait de la concurrence intraspécifique élevée. — Si le terrain est vraiment inondé par l'eau de pluie, on y trouve le *Deschampsietum mediae* (BRAUN-BLANQUET 1924, BRAUN-BLANQUET et PAWLOWSKI 1931).

Les conditions hydrologiques favorables à l'établissement du *Rosmarineto-Lithospermetum schoenetosum* sont réalisées dans les stations, qui ont un sous-sol imperméable, et qui sont localisées soit sur la voie de la drainage d'une colline, soit dans des cuvettes situées à proximité d'une ligne de partage des eaux.

Le sous-sol imperméable est réalisé en Bas-Languedoc surtout par les marnes lacustres de l'Éocène et du Crétacé supérieur: marnes rouge-brique ou jaunes du Rognacien, marnes tachetées jaune-rose-violet-gris du Lutétien supérieur et marnes jaunes bariolées du Bartonien. Le *Rosmarineto-Lithospermetum schoenetosum* est lié si strictement à ces marnes, qu'il peut servir d'indicateur local pour celles-ci.

Ces marnes sont intercalées entre des calcaires, grès et conglomérats marneux un peu plus perméables et n'affleurent presque jamais sur de grandes étendues ininterrompues. Ce n'est qu'au Nord de l'abbaye de Vallemagne, le long de la route de St. Pons, que de grandes étendues de *Rosmarineto-Lithospermetum schoenetosum* ont été repérées sur les marnes rouges du Rognacien.

Sur les sédiments entre lesquels les marnes sont intercalées on trouve soit le *Quercetum cocciferae rosmarinetosum* (Braun—Blanquet 1935), soit le *Rosmarineto-Lithospermetum ericetosum, helianthemetosum* ou *pinetosum* (G. Braun-Blanquet 1936), soit une végétation, qui se range plus ou moins dans l'*Aphyllantheto-Leontodetum Villarsii* (Braun-Blanquet 1931, Tomaselli 1948). Il faut absolument se garder d'une conclusion erronée en ce qui concerne l'évolution en se basant sur l'arrangement des types de végétation sur le terrain, cet arrangement pouvant être la conséquence de la variation du sous-sol.

Le sol du *Rosmarineto-Lithospermetum schoenetosum* peut être caractérisé par le profil suivant, qui est une généralisation de sept profils représentatifs:

A_0 0—4 cm, seulement sous buissons ou comme débris de souches. Litière principalement formée de feuilles de *Rosmarinus officinalis*, *Erica multiflora*, *Buxus sempervirens* et de débris de souches et tiges de *Schoenus nigricans* et *Aphyllanthes monspeliensis*. Diplopodes et fourmis sont fréquents. —
Manque dans les espaces ouverts où il est souvent remplacé par une carapace de cailloutis (en anglais "erosion pavement"). Limon colluvial blanchâtre ou jaune crevassé.

A_1 10—20 cm, brun grisâtre, bien grumelé et aéré, enracinement fort, squelette fin, lombrics fréquents, microflore riche (surtout *Streptomyces* spec.).

A_2 d'épaisseur variable, en général brun foncé ou ocre, plus compact que A_1, squelette plus grossier parfois stratifié, enracinement de *Schoenus* et des arbustes assez fort.

Ca/G Zone de marnes à efflorescences calcaires blanches et taches de gley; cet horizon manque souvent.

C/G Marnes rouges ou jaunes, tendres, très peu perméables, à cassure polyédrique, à taches grises de gley, sans racines (sauf de *Rosmarinus*) et sans cailloux. Cet horizon se trouve en général à une assez faible profondeur (25 cm environ), tout au plus à 70 cm environ et cela seulement sur des terrains de faible inclinaison.

Le contenu en carbonates de ce sol est élevé. Des mesures dans un profil sur marnes lutétiennes ont révélé un pH 7,5 et 40 % de $CaCO_3$ pour l'horizon A_2, un pH 8,4 et 60 % de $CaCO_3$ pour l'horizon C/G. Ces mesures ne sont pas nécessairement représentatives. (Voir également G. Braun-Blanquet 1936).

Discussion du profil:

Le sol du *Rosmarineto-Lithospermetum schoenetosum* est dégradé, le profil primitif étant enlevé aux trois quarts par l'érosion. Le

Rosmarineto-Lithospermetum schoenetosum ne s'installe que sur des sols de faible profondeur.

Les horizons supérieurs contiennent un squelette de cailloux, lequel manque dans le horizon C. Ce fait peut indiquer que le sol est, du moins en partie, un sol colluvial. Mais il est plus probable que ces cailloux ne sont que les restes de conglomérats ou calcaires marneux, qui ont reposé sur les marnes et ont été enlevés. Si l'équilibre "érosion-accumulation" tend vers l'accumulation, on voit parfois des "pavés" ensevelis dans le profil.

Les efflorescences de $CaCO_3$ indiquent une remontée des solutions salines pendant la période de sécheresse.

Les lombrics et la forte odeur de *Streptomyces* spec., dont la présence abondante a été confirmée par des cultures, indiquent une bonne aération.

Les taches grises de réduction indiquent, que le drainage vertical est empêché.

Le classement exact de ce type de sol — dénommé par Braun—Blanquet (1947) "terre jaune méditerranéenne" — n'est pas encore établi; il y a certaines affinités avec les rendzines.

Tout le complexe de la "terre jaune méditerranéenne" est très érodable, surtout l'horizon A_2. L'érosion à l'intérieur des autres sous-associations du *Rosmarineto-Lithospermetum* est très accusée, mais elle se borne souvent à l'érosion laminaire (sheet erosion, Flächenerosion). Dans les stations de la sous-association *schoenetosum* l'érosion peut être particulièrement intense avec une tendance nette vers le ravinement (gully erosion). Ce ravinement peut produire des ravins de dimensions considérables et peut aller jusqu'à l'enlèvement complet des marnes pour mettre à nu les couches rocheuses sous-jacentes. Sur les bords de nombreux rigoles et ravins d'érosion dans les marnes on trouve les fragments d'un *Rosmarineto-Lithospermetum schoenetosum* en voie de destruction.

Quelles sont les conséquences pour la végétation? Par la présence de marnes imperméables à faible profondeur il y a de l'eau stagnant pendant les pluies; le drainage ne peut être donc que latéral. L'écoulement (run-off) provoque l'érosion, élimine beaucoup de plantules et déchausse les plantes adultes mal enracinées. D'un autre côté le dépôt de matières détritiques (par exemple 1 cm par pluie d'après nos observations) [1] peut être tout aussi funeste pour les plantules que l'érosion. Après les pluies le sol reste encore quelque temps humide. (Drainage de la pente en amont; sous-sol moins perméable que dans les stations des autres sous-associations). Enfin le sol peu profond se déssèche, le drainage étant accompli.

A ces données surtout qualitatives devraient s'ajouter des données quantitatives sur la température, l'évaporation, la luminosité, la composition physique du sol, son contenu en eau au courant de l'année etc. Nous renvoyons le lecteur à la thèse de R. Tomaselli sur la pelouse à *Aphyllanthes* (1948, p. 31), dont les données écologiques quantitatives sont, jusqu'à un certain degré, applicables au *Rosmarineto-Lithospermetum schoenetosum*.

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[1] M. le Dr Braun–Blanquet nous a communiqué qu'il y avait parfois 10 cm par orage (novembre 1951).

4. ENRACINEMENT

Dans une végétation qui doit faire face à l'érosion l'enracinement est d'une importance toute particulière et explique en partie le comportement des différentes espèces et la structure de la végétation. Quelques systèmes radiculaires dans le *Rosmarineto-Lithospermetum schoenetosum* ont pu être observes.

C'est ainsi que nous avons pu distinguer trois types d'enracinement de *Schoenus nigricans:*

1. Touffes plus ou moins vigoureuses à souches horizontales et racines surtout verticales en "queue de cheval" dense. C'est le type d'érosion.
2. Touffes généralement peu denses à souches verticales et à entrenoeuds allongés. Les racines, qui sortent des noeuds à différentes hauteurs, ne forment pas de "queue de cheval": C'est le type colluvial extrême.
3. Touffes petites à courtes souches horizontales et à racines verticales et horizontales, ces dernières constituant un réseau dense: c'est le type "pelouse" de l'*Inuleto-Schoenetum* bien fixé.

Ces types reflètent bien le milieu:

Racines profondes bien ancrées dans le type d'érosion, qui souffre de la sécheresse dès le commencement de l'été. On peut imaginer que, pendant cette sécheresse, les racines les plus intérieures de la touffe subissent la concurrence la plus forte de leurs voisines, ce qui pourrait provoquer la mort du centre de la touffe.

La souche verticale est un moyen d'éviter l'ensevelissement sous les matières colluviales laissées par le ruissellement. Ces souches donnent une idée du dépôt de matières détritiques. Dans des ravins d'érosion près de Piquet Guérin nous avons dégagé des touffes à souches de cinq à six entrenoeuds verticaux, chaque entrenoeud ayant 4—5 cm de longueur.

Le type "pelouse" enfin pourrait refléter l'humidité persistante du sol et la mauvaise aération de ses couches plus profondes. Sur l'île néerlandaise de Schiermonnikoog nous avons dégagé d'un sol couvert d'une couche d'algues et mal aéré une touffe de *Schoenus* avec les mêmes racines pour la plupart horizontales.

Schoenus nigricans peut très bien retenir le sol entre ses racines, mais, excepté dans le type "pelouse", seulement sous la touffe même.

Carex glauca est au contraire mal adaptée à l'érosion. Ses longs stolons portent de faibles racines fasciculées aux noeuds. En cas d'érosion *Carex glauca* déchaussée, reposant sur ses stolons comme sur des échasses, les racines dans l'air, meurt. Cela a pu être observé clairement au pied Nord du Pic Saint Loup. *Carex glauca* a une valeur comme indicatrice de l'absence locale de l'érosion.

Rosmarinus officinalis possède une forte racine pivotante qui pénètre jusque dans le sous-sol. Elle est bien propre à fixer solidement la plante et à puiser l'eau, mais elle retient mal le sol. Tandis que l'érosion laisse les touffes de *Schoenus* sur de petits socles, elle met à nu la racine de *Rosmarinus*. Une plante adulte de *Rosmarinus* est bien résistante contre ce déchaussement, mais il faut du temps pour que cette racine profonde soit formée (voir aussi BRAUN—BLANQUET 1924).

Ceci est également valable pour *Lithospermum fruticosum* et *Juniperus oxycedrus*. Ce dernier est même si résistant que des pousses feuillues apparaissent sur ses racines entièrement dénudées. Mais toutes ces espèces doivent passer le stade vulnérable de leur jeunesse.

Erica multiflora a des plantules à racines tendres et déjà GIROUX (1934) constate l'enracinement peu profond des individus adultes. *Teucrium polium* a une souche à racines tendres. Ceci explique la préférence de ces espèces pour les îlots de *Schoenus*.

Coris monspeliensis a de petites racines coudées et pivotantes assez profondes.

Aphyllanthes monspeliensis et *Carex humilis* ont l'enracinement semblable au type d'érosion de *Schoenus nigricans* mais sur une plus petite échelle.

Fumana ericoides et *Fumana thymifolia* émettent plusieures racines coudées et pivotantes pénétrant profondément dans le sol. (Voir aussi TOMASELLI 1948).

5. DISCUSSION DU TABLEAU DE RELEVÉS

Les relevés de notre tableau sont arrangés selon le critère "érosion" ou "accumulation". Il ressort du tableau qu'en cas d'érosion prépondérante *Carex glauca*, une espèce des espaces ouverts, manque presque complètement, tandis qu'on la trouve presque toujours lorsque l'accumulation est prépondérante. Les raisons pour ce comportement ont été expliqué dans le chapitre sur l'enracinement. *Phillyrea angustifolia*, une espèce des îlots, a la même tendance, bien que moins nette, pour des raisons encore inconnues.

Il y a donc lieu de distinguer une variante "d'érosion" sans *Carex glauca*, c'est la variante "typique", et une autre variante "d'accumulation" (ou sans érosion), dite "à *Carex glauca*".

Linum campanulatum est une espèce méditerranéo-montagnarde qui évite la plaine, tandis que *Erica multiflora* ne sort pas de celle-ci. Voilà la raison pour laquelle *Erica multiflora* manque dans les trois relevés pris au Nord du Pic Saint Loup, alors que *Linum campanulatum* est noté seulement dans ces trois relevés.

Argyrolobium Linnaeanum, *Avena bromoides*, *Asperula cynanchica* et *Thesium divaricatum*, si communs dans le *Rosmarineto-Lithospermetum ericetosum*, sont assez rares dans le *Rosmarineto-Lithospermetum schoenetosum*. Par contre *Trinia glauca* et *Thymus angustifolius* ont une préférence nette pour ce groupement.

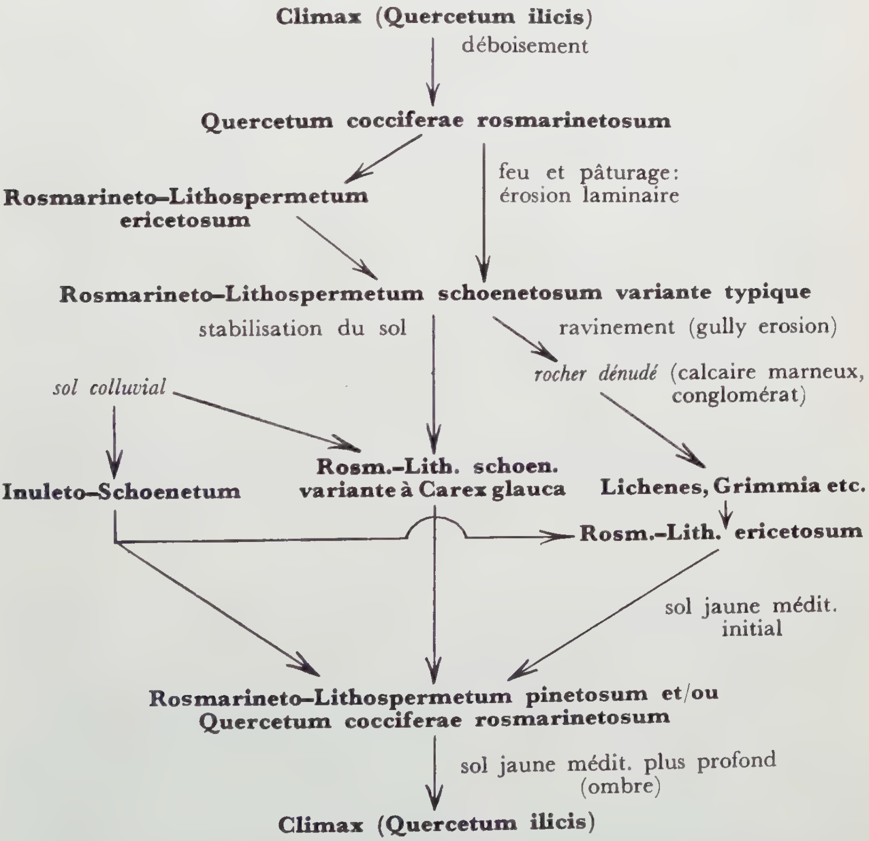
Schoenus nigricans et *Andropogon gryllus* peuvent être considérés comme espèces différentielles du *Rosmarineto-Lithospermetum schoenetosum* par rapport aux autres sous-associations de l'association. Ils indiquent tous deux l'humidité temporaire du sol.

Si l'on excepte quelques rares pullulations printannières de *Draba verna*, *Hutchinsia petraea*, *Cerastium pumilum* etc., dues au remaniement du sol par les lombrics, l'absence de tout thérophyte est remarquable.

6. ÉVOLUTION

Sous la protection de *Schoenus nigricans* bon nombre d'espèces se maintiennent malgré une forte érosion laminaire, alternant ou non avec l'ensevelissement. Puisque *Schoenus nigricans*, *Stipa juncea* et *Carex humilis* ont tendance à former de petites terrasses et barrages, l'érosion laminaire est freinée jusqu'à un certain degré. Par contre la végétation est trop ouverte pour pouvoir résister au ravinement. Si l'hydrologie du terrain n'est pas trop défavorable les petits barrages du *Rosmarineto-Lithospermetum schoenetosum* sont suffisants pour fixer le sol sur les pentes inférieures à cinq degrés. La régénération du tapis

ÉVOLUTION DE LA VÉGÉTATION SUR LES MARNES DU BAS-LANGUEDOC


Climax (Quercetum ilicis)
déboisement
Quercetum cocciferae rosmarinetosum
Rosmarineto–Lithospermetum ericetosum
feu et pâturage: érosion laminaire
Rosmarineto–Lithospermetum schoenetosum variante typique
stabilisation du sol
ravinement (gully erosion)
rocher dénudé (calcaire marneux, conglomérat)
sol colluvial
Inuleto–Schoenetum
Rosm.–Lith. schoen. variante à Carex glauca
Lichenes, Grimmia etc.
Rosm.–Lith. ericetosum
sol jaune médit. initial
Rosmarineto–Lithospermetum pinetosum et/ou Quercetum cocciferae rosmarinetosum
sol jaune médit. plus profond (ombre)
Climax (Quercetum ilicis)

On sait que le développement d'un profil de sol nouveau dure incomparablement plus longtemps que l'érosion du profil, fait sur lequel on ne peut jamais assez insister.

végétal en direction du climax est alors amorcée. Ceci se traduit par l'apparition de jeunes *Quercus coccifera* et *Pinus halepensis*, alors qu'en cas d'érosion on ne trouve que des individus adultes épargnés.

Le résultat d'une régénération en direction du climax a été rencontré près de Piquet Guérin sous forme d'une forêt de *Pinus halepensis*, renfermant encore *Schoenus nigricans*, *Erica multiflora*, *Rosmarinus officinalis*, *Genista Jordani*, *Globularia Willkommi*, *Carex glauca*, *Carex humilis* et d'autres espèces du *Rosmarineto-Lithospermetum schoenetosum*, et même *Viburnum tinus*, *Smilax aspera* et *Rubia peregrina*, espèces appartenant au climax, le *Quercetum ilicis galloprovinciale*.

Lorsque le ravinement a fait du progrès dans les marnes, le rocher dur sous-jacent est presque toujours mis à nu: l'installation d'un sol nouveau commence. D'abords apparaissent des Lichens, ensuite des mousses, surtout *Grimmia pulvinata* et *Grimmia orbicularis*, qui forment de petites monticules remplies de terre fine, qui permet la germination de certaines espèces. Mais on observe aussi des plantules de *Rosmarinus officinalis*, *Thymus vulgaris*, *Lithospermum fruticosum*, *Buxus sempervirens*, *Erica multiflora* et *Rhamnus alaternus* dans des fentes du rochter et dans les dépressions à l'abri du ruissellement. Ces espèces indiquent le développement ultérieur vers le *Rosmarineto-Lithospermetum ericetosum*.

Il semble probable que le *Rosmarineto-Lithospermetum* qui se développe après la destruction par l'homme du *Quercetum cocciferae rosmarinetosum* prend immédiatement l'aspect d'un *Rosmarineto-Lithospermetum schoenetosum*, mais celui-ci peut également provenir d'un *Rosmarineto-Lithospermetum ericetosum*.

C'est ainsi qu'on peut esquisser le schema ci-dessus.

7. DISTRIBUTION GÉOGRAPHIQUE

Nous avons repére le *Rosmarineto-Lithospermetum schoenetosum* dans le Bas-Languedoc de la région de Villeveyrac à l'Ouest jusqu'à Prades-le-Lez à l'Est et jusqu'au versant septentrional du Pic Saint Loup au Nord. Il est possible que le *Rosmarineto-Lithospermetum schoenetosum* existe également plus au NE, où il y a d'autres affleurements de marnes éocènes. La limite d'altitude semble se situer vers 200 m. MOLINIER (1935) ne signale pas de groupement semblable de la Provence occidentale.

8. CONSIDÉRATIONS PRATIQUES

Le *Rosmarineto-Lithospermetum schoenetosum* peut servir:

a) au géologue comme indicateur des marnes tendres

b) au forestier comme indicateur d'un sol peu profond à drainage vertical empêché et exposé au ravinement imminent.

Même après le reboisement, la menace du ravinement subsiste sur les marnes tendres et il faut exploiter la pineraie sur ces marnes avec beaucoup de prudence. Le bois près de la propriété Piquet Guérin (Route de Ganges) en est un exemple frappant.

Pour arrêter l'aggravation du ravinement on pourrait élever de petits barrages de pierres dans les ravins et planter le *Schoenus nigricans*, comme on le fait avec l'*Ammophila arenaria* dans les dunes hollandaises.

Le *Schoenus nigricans* un peu plus serré que dans le *Rosmarineto-Lithospermetum* naturel pourrait aider à retenir le sol; il survit à l'ensevelissement.

En terminant cette étude il nous est un devoir agréable d'exprimer notre profonde gratitude à Moniseur le Dr. J. Braun–Blanquet, Directeur de la Station Internationale de Géobotanique Méditerranéenne et Alpine, qui nous a initié dans la flore méditerranéenne et nous a fait profiter de sa riche expérience.

Le second auteur remercie le Ministre de l'Education, des Beaux-Arts et des Sciences (Minister van Onderwijs, Kunsten en Wetenschappen) au Gouvernement néerlandais pour la bourse dont il a bénéficie.

Nous remercions très sincèrement Monsieur L. Ferlan (de Montpellier), qui nous a transmis des relevés et notes concernant notre sujet et qui a mis à notre disposition quelques-uns de ses beaux dessins.

Nous devons à Monsieur M. E. D. Poore (de Cambridge) des observations sur les germinations. Monsieur M. van Oosten (de Wageningen) a contribué à l'étude de l'enracinement. Bien des fois nous avons parcouru ensemble le terrain.

Monsieur G. Heim a bien voulu corriger le texte français du manuscrit; nous lui en sommes très reconnaissants.

Summary

An account is given of some aspects of a mediterranean shrub-vegetation. Attention has been paid to its floristical composition, its peculiar structure (partly due to an abnormal kind of tussock formation by *Schoenus nigricans*), its soil, its root-systems and its dynamism. This vegetation indicates imminent gully erosion and the presence of soft impermeable marls at shallow depth.

Données appartenant au tableau de relevés

Légende: A = Auteur(s), D = Date, L = Localité, Ss = Sous-sol, Cp = Conditions pédologiques (Seulement les éléments les plus importants des notes pédologiques ont été inclus), pavé = couvert d'une carapace de cailloutis.

VARIANTE TYPIQUE

Relevé N. 5: A: Braun–Blanquet et Ferlan. D: 26.3.50. L: Grabels, à gauche du chemin menant à Bel Air. Ss: Rognacien sup., marnes rouges. Cp: Érodé, pavé.

Relevé N. 14: A: Ferlan. D: 6.6.50. L: Grabels, au Nord de la bifurcation du chemin menant à Bel Air. Ss: Rognacien sup., marnes rouges. Cp: Érodé, pavé.

Relevé N. 48: A: van Oosten et Zwillenberg. D: 25.4.51. L: Grabels, à droite de la bifurcation Bel Air, à gauche du chemin. Ss: Rognacien sup., marnes rouges. Cp: Érodé, pavé, marnes presque à nu.

Relevé N. 19: A: de Wit et Zwillenberg. D: 29.3.51. L: Au Nord de la Soucarède (région de Grabels). Ss: Rognacien sup., marnes rouges. Cp: Érodé, pavé, marnes (C/G) à 23 cm, beaucoup de lombrics.

Relevé N. 32: A: Zwillenberg. D: 15.4.51. L: À l'Est de la Soucarède (région de Grabels). Ss: Rognacien sup., marnes rouges. Cp: Érodé, pavé, marnes (C/G) à 20 cm, A_2 manque.

Relevé N. 17: A: Braun–Blanquet et de Wit. D: 26.3.51. L: Bifurcation d'un ruisseau dans le Vallon de Grabels. Ss: Rognacien sup., marnes rouges. Cp: Pavé, érosion accompagnée d'une accumulation partielle de sol.

Relevé N. 7: A: Ferlan. D: 3.5.50. L: Tour Piquet, au NW de la propriété Piquet Guérin. Ss: Lutétien sup., marnes bigarrées. Cp: Érodé, pavé.

Relevé N. 9: A: Braun–Blanquet et Ferlan. D: 15.5.50. L: N. de Clapiers, SE de Prades-le-Lez. Ss: Lutétien sup., marnes bigarrées. Cp: Érodé, pavé.

Relevé N. 38: A: Zwillenberg. D: 19.4.51. L: Tour Piquet, au NW de Piquet Guérin. Ss: Lutétien sup., marnes bigarrées. Cp: Érodé, pavé, marnes (C/G) à 10 cm, beaucoup de Diplopodes.

Relevé N. 24: A: Braun–Blanquet, van Oosten, Poore, de Wit et Zwillenberg. D: 6.4.51. L: Mas Vinaigre, Colline de la Sentinelle. Ss: Rognacien inférieur, marnes jaunes. Cp: Pavé, érodé avec une légère accumulation, C/G à 50 cm.

Relevé N. 58: A: Zwillenberg. D: 12.5.51. L: Vallemagne, au Nord de l'abbaye, route sur St. Pons. Ss: Rognacien sup., marnes rouges. Cp: Pavé, fortement érodé, profondeur du sol faible.

VARIANTE À CAREX GLAUCA

Relevé N. 50: A: van Oosten et Zwillenberg. D: 26.4.51. L: le long du ruisseau principal du Vallon de Grabels. Ss: Rognacien sup., conglomérats et marnes rouges. Cp: Sol colluvial non-horizonté, beaucoup de lombrics et fourmis.

Relevé N. 10: A: Ferlan. D: 20.5.50. L: Bel Air, à droite de la route pour St. Paul. Ss: Rognacien sup., conglomérats et marnes jaunes. Cp: Sol colluvial non-horizonté dans un bas-fond.

Relevé N. 11: A: Ferlan. D: 20.5.50. L: À l'Est de Montarnaud entre deux collines. Ss: Rognacien sup., conglomérats et marnes jaunes. Cp: Accumulation de sol colluvial dans un bas-fond.

Relevé N. 40: A: Poore, van Oosten, de Wit et Zwillenberg. D: 22.4.51. L: Bel Air, sous le sommet d'une colline à gauche du chemin pour Grabels. Ss: Rognacien sup., marnes jaunes entre conglomérats. Cp: Accumulation faible de sol colluvial sur un petit plateau marneux, Ca/G à 23 cm, faiblement pavé.

Relevé N. 41: A: de Wit et Zwillenberg. D: 22.4.51. L: Bel Air ibidem, ± 150 m plus au Nord que No. 40. Ss: Rognacien sup., marnes jaunes entre conglomérats. Cp: Ca/G à 23 cm, eau stagnante au printemps: en surface limon blanchâtre, crevassé, encore très humide; Schoenus très bas.

Relevé N. 8: A: Ferlan. D: ?.?.1950. L: Fontfroide, au Sud de la carrière. Ss: Lutétien sup., marnes bigarrées. Cp: Accumulation de sol colluvial au fond d'un ravin d'érosion.

Relevé N. 51: A: van Oosten et Zwillenberg. D: 27.4.51. L: Fontfroide, au Sud de la carrière. Ss: Lutétien sup., marnes bigarrées. Cp: Accumulation de sol colluvial sur pente faible, C/G à 25 cm.

Relevé N. 53: A: Zwillenberg. D: 6.5.51. L: Tour Piquet, au NW de Piquet Guérin. Ss: Lutétien sup., marnes bigarrées. Cp: Fond d'une rigole d'érosion, sol colluvial très fin, non-horizonté, crevassé en surface.

Relevé N. 56: A: Zwillenberg. D: 6.5.51. L: Tour Piquet, au NW de Piquet Guérin. Ss: Lutétien sup., marnes bigarrées. Cp: Accumulation active de sol colluvial, marnes à 50 cm, pavés ensevelis.

Relevé N. 57: A: Zwillenberg. D: 6.5.51. L et Ss comme N. 56. Cp: Sol colluvial faiblement érodé, pavé, végétation en petits barrages.

Relevé N. 61: A: Zwillenberg D: 15.5.51. L: 1 km à l'Est du Mas de Garonne, versant Nord du Pic Saint Loup. Ss: Bartonien, marnes bariolées. Cp: Horizon C marneux-squelettique (colluvial?) à 50 cm, très humide par les suintements de la pente.

Relevé N. 62: A: Zwillenberg. D: 15.5. 51. L et Ss comme N. 61. Cp: Marnes autochtones à 15 cm, pavé, dépassé par des rigoles d'érosion (il n'y a plus d'érosion laminaire).

Relevé N. 63: A: Zwillenberg. D: 15.5.51. L et Ss comme N. 61. Cp: Pas de profil creusé. Situé sous un affleurement rocheux (barrage contre le ruissellement).

Accidentelles:

Hieracium Wiesbaurianum Uechtr.: N. 10 (R), N. 61 (+).
Rubia peregrina L.: N. 51 (1.2)
Smilax aspera L.: N. 51 (+)

Lonicera implexa Aiton: N. 51 (+.1)
Pistacia lentiscus L.: N. 51 (+)
Quercus ilex L.: N. 62 (+.2)
Poa bulbosa L.: N. 9 (2.3)
Deschampsia media (Gouan) Roem et Sch.: N. 8 (+)
Rosa sempervirens L.: N. 53 (+)
Anacamptis pyramidalis (L.) Rich.: N. 63 (1.1)
Platanthera bifolia (L.) Rich.: N. 63 (+.1)

La classification des espèces caractéristiques, représentée dans le tableau, est basée, en ce qui concerne *l'Aphyllanthion* sur la thèse de R. Tomaselli (1948), et en ce qui concerne les autres unités sur les données de la Station Internationale de Géobotanique Méditerranéenne et Alpine à Montpellier (mai 1951).

BIBLIOGRAPHIE

Braun-blanquet, J., Études sur la végétation méditerranéenne III, Bull. Soc. Bot. de France 71, 1924, p. 879.

Braun-Blanquet, J., Pflanzensoziologie, Berlin 1928.

Braun-Blanquet, J., Aperçu des Groupements Végétaux du Bas-Languedoc, Rapport sur l'année 1930, 4. S.I.G.M.A. Comm. No. 9, 1931.

Braun-Blanquet, J., Un problème économique et forestier de la Garigue languedocienne. S.I.G.M.A. Comm. No. 35, 1935.

Braun-Blanquet, J., La Chênaie de Yeuse méditerranéenne. S.I.G.M.A. Comm. No. 45, 1936.

Braun-Blanquet, J., Le Tapis végétal de la Région de Montpellier et ses rapports avec les sols. S.I.G.M.A. Comm. No. 94, 1947.

Braun-Blanquet, J., N. Roussine et R. Nègre: Les Groupements Végétaux de la France Méditerranéenne. C.N.R.S. Service de la Carte des Groupements Végétaux de la France (sous presse).

Braun-Blanquet, G., La Lande à Romarin et Bruyère (Rosmarino-Ericion) en Languedoc. S.I.G.M.A. Comm. 48, 1936.

Braun-Blanquet, J., L. Emberger et R. Molinier, Instructions pour l'établissement de la carte des groupements végétaux de la France. C.N.R.S., Service de la carte des groupements végétaux de la France, Montpellier 1947.

Braun-Blanquet, J. et B. Pawlowski, L'eau et l'air du sol dans l'association à Deschampsia media et Brunella hyssopifolia. S.I.G.M.A. Comm. No. 10, 1931.

Giroux, J., Erica multiflora ou "Bruyère à fleurs nombreuses", S.I.G.M.A. Comm. No. 27, 1934.

Molinier, R., Études Phytosociologiques et Écologiques en Provence Occidentale. S.I.G.M.A. Comm. No. 35*a*, 1935.

Tomaselli, R., La pelouse à Aphyllanthes (Aphyllanthion) de la garigue montpelliéraine. Atti dell'Inst. Bot. e del Lab. Crittogam. della Univ. di Pavia, Serie 5, Vol. 7 (2). S.I.G.M.A. Comm. No. 99, 1948.

Carte géologique de la france 1 : 80,000 deuxième édition, feuille No. 233 (Montpellier) et feuille No. 221 (le Vigan).

NOTE

La *Potentilla verna* L. figurant dans le tableau est la variété *australis* Wolff de cette espèce. — D'après un article sous presse de Mme. N. Roussine (Rec. Trav. Lab. Bot. Géol. et Zool. Fac. d. Sc. Univ. Montpellier, Série Bot., Fasc. 5) le méconnu *Thymus angustifolius* Pers. du *R. L. schoenetosum* est une nouvelle espèce: *Thymus Embergeri* Roussine (2n = 48).

Rosmarineto-Lithospermetum SCHOENETOSUM

	variante typique											variante à Carex glauca												
Numéro du relevé	5	14	48	19	32	17	7	9	38	24	58	50	10	11	40	41	8	51	53	56	57	61	62	63
Exposition	N	WNW	NNE	NNW	ESE	N	SW	NW	WSW	SE	N	/	NW	/	E	/	W	SSW	/	/	/	ESE	E	E
Inclinaison (°)	5	5	15	10	8	2	5	5	8	1	5-7	0	5	0	1	0	5	5	0	0	<1	3-5	3	10
Surface du relevé (m²)	100	50	50	100	50	50	50	50	25	30	20	50	50	50	50	50	50	100	25	25	30	50	50	16
Recouvrement (%)	70	70-80	40	50	75	60	60	70-75	40	60	50	80	90	100	70	80	80	80	60-70	45	70	70	70	50-60
Hauteur de la végétation (cm)	40-60	30-35	50	50	50	50	30	30	40	50	30-40	50-60	40-50	50-70	50	50	30-60	50-60	70-80	50-70	50	50-70	70	50
Caractéristiques du Rosmarineto-Lithospermetum (J.Br.-Bl.1924)G.Br.-Bl.1936 :																								
Lithospermum fruticosum L.	.	.	+.2	R	+.1	.	+	+	+.1	.	R	+.1	+.2	.	.	.	.	+	.	.	.	.	(+)	.
Sideritis scordioides L.	+	.	+.1	.	.	+.1	.	.	.	.	.	.	+.1	.	.	.	.	.	.	.	.	.	.	.
Erica multiflora L.	+.2	1.2	1.2	2.2	1.2	3.3	3.3	.	3.3	3.2	2.2	3.2	+.3	4.4	3.2	4.3	.	2.2	3.3	3.3	3.2	.	.	.
Caractéristiques de l'alliance Rosmarino-Ericion (J.Br.-Bl.1931)G.Br.-Bl.1936 :																								
Coris monspeliensis L.	+	+	+.1	.	+.1	.	+	2.2	1.1	.	.	.	+	.	+.1	.	+	1.2	.	+.1	.	1.1	+.1	+.1
Rosmarinus officinalis L.	2.2	1.2	+.2	1.1	1.2	1.2	2.2	2.2	2.2	1.2	1.2	2.2	2.3	.	2.2	2.2	2.2	+.2	+.1	1.2	1.1	1.2	3.3	1.2
Staehelina dubia L.	+	+	+.1	+.1	+.1	.	+	+	1.1	+.1	1.2	.	+	.	.	.	+	2.2	.	1.1	.	.	.	.
Stipa juncea L.	.	.	.	.	3.2	+.2	+	+.2	(+.1)	.	1.2	1.2	+	.	+.2	1.2	.	.	.	.	.	.	.	+.2
Genista Jordani Shuttlew.	1.1	.	.	1.1	1.1	1.1	1.2	+.2	1.1	1.1	+.2	1.1	1.1	.	1.2	+.1	1.2	+.2	1.2	1.1	+.1	+.2	.	+.2
Pinus halepensis Mill.	.	.	.	R	.	.	+.1	+	R	+	+.1	.	.	.	.	.	.	1.1(j)	+.1	.	.	.	.	.
Caractéristiques de l'Aphyllantheto-Leontodetum Villarsii (J.Br.-Bl.1931)Tom.48																								
Thymus angustifolius Pers.	+.2	+.2	+.1	.	.	+.1	+.2	1.2	+.1	.	.	+	2.2	.	1.2	1.1	.	.	.	.	+.2	1.2	1.1	1.1
Stipa mediterranea A. et G.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Caractéristiques de l'alliance Aphyllanthion (J.Br.-Bl.1931)Tomaselli 1948 :																								
Aphyllanthes monspeliensis L.	+	+	+.2	+.2	+.2	.	1.2	2.3	+.2	.	+.2	2.2	1.2	2.2	+.2	1.2	+	2.2	.	+.2	+.2	1.2	1.2	1.2
Globularia Linnaei Ry.	1.1	+	+.2	R	+.1	.	+	+	.	2.2	(+)	.	+	.	1.2	2.1	.	+.2	.	+.1	+.2	+.2	1.2	.
Potentilla verna L.	1.1	+	+.2	.	.	+.1	.	.	.	.	.	.	.	+	+.1	+.1	+	+.2	1.1	.	+.2	.	1.2	.
Chrysanthemum graminifolium ssp. controversum Lor. et Barr.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1.1	1.1	+.1
Catananche coerulea L.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Lotus corniculatus var. villosus Brand.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+.1	.	.	.	+.1	.	.	.	.	.
Caractéristiques de l'ordre Rosmarinetalia J.Br.-Bl. 1931 :																								
Fumana ericoides (Cav.) Pau	2.1	+	1.2	1.1	1.2	1.1	1.2	2.2	1.1	1.1	1.1	1.1	1.2	+	1.1	1.1	+	1.2	+.2	1.1	.	1.1	1.1	1.1
Lavandula latifolia (L.) Villars	1.1	1.2	+.1	.	.	+	+	1.2	.	(+)	1.1	+.2	+	.	+.2	.	1.1	.	.	+.2	+.1	+.1	1.1	.
Euphorbia nicaeensis All.	+	.	+.1	.	.	+	+	.	.	(+)	+	+.2	+	.	.	.	+	+	.	.	.	+.1	+.1	+.1
Leontodon Villarsii Lois.	+	+	.	.	.	.	+.2	.	.	.	+	.	+	.	.	.	.	.	.	.	.	+.2	.	.
Avena bromoides Gouan	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	R	.	.	+.2	.	.	.	.	.
Centaurea conifera L.	.	+	.	.	.	+.1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+.1	+.1	.
Linum campanulatum L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1.1	1.1	+.1
Helianthemum italicum (L.) Pers.	+	.	1.2	+.1	+.1	.	.	.	.	.	.	.	.	.	1.2	.	.	.	.	.	.	+.1	1.1	.
Caractéristiques de la classe Ononido-Rosmarinetea J.Br.-Bl. 1947 :																								
Carex humilis Leyss.	1.2	+.2	1.2	1.2	+.2	2.2	1.2	2.2	1.2	1.2	+.2	2.2	2.2	.	1.2	.	2.3	2.2	.	+.2	1.2	1.2	1.2	1.2
Koeleria vallesiana (Sut.) Gaud.	1.1	+.2	+.2	.	.	.	+.2	+.2	+.2	.	(+.2)	+.2	+	+	+.2	1.2	1.2	.	.	.	.	+.2	+.2	+.2
Trinia glauca (L.) Dumort.	1.2	+	1.2	.	+.1	.	.	+	+.1	.	(+.1)	+.2	.	.	.	.	1.2	.	+.1	.	+.1	+.1	1.1	+.1
Helianthemum canum (L.) Baumg.	.	1.2	.	1.1	.	1.2	.	.	.	.	.	.	1.2	.	.	.	.	.	.	.	.	1.1	+.1	.
Coronilla minima L.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+.1	.	.
Asperula cynanchica (Bauhin) L.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Différentielles de la sous-association Rosm.-Lithospermetum schoenetosum :																								
Schoenus nigricans L.	3.3	2.3	2.2	3.3	1.2	2.2	3.3	3.3	2.2	2.2	2.2	2.2	3.3	3.3	3.2	3.3.	3.2	3.3	2.3	2.3	1.2	3.3	2.3	2.2
Andropogon gryllus L.	.	.	.	.	.	(+.2)	.	+	.	.	.	.	.	+.2	1.2	1.2	1.2	.	.	.	3.2	+.2	.	.
Différentielles de la variante à Carex glauca du Rosm.-Lith.schoenetosum :																								
Carex glauca Murr.	.	.	.	.	.	.	.	.	.	.	+.2	1.2	.	2.1	+.1	1.2	1.1	+.1	1.2	1.1	+.2	1.1	1.1	+.2
Phillyrea angustifolia L.	.	.	.	.	.	.	.	.	.	+.1	.	+	.	+	+.2	+.2	+	+.2	1.1	+	.	.	.	.
Compagnes :																								
Inula viscosa (L.) Aiton	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+.2	.	+.2	.	.	.
Brachypodium phoenicoides R. et S.	R	.	.	.	.	+.2	+.2	.	.	+.2	.	.	.	.	.	+.2	+	.	.	.	.	+.2	.	.
Brachypodium ramosum (L.) R. et S.	.	.	.	.	.	1.2	.	+°°	.	+.2	.	.	R	.	.	.	.	1.2	.	.	.	.	+.2	+.2
Molinia coerulea (L.) Moench.	.	.	.	.	.	.	+	.	1.2	.	.	+.2°	.	+	.	.	.	.	2.3	2.3	.	.	.	.
Festuca duriuscula L.	1.1	+.2	.	+.2	.	.	+.2	1.2	.	+.2	.	+.2	+.2	+	+.2	.	1.1	+.1	1.2	1.2	.	1.2	1.2	1.2
Bromus erectus Huds.	.	+	.	.	+.2	.	.	.	.	.	.	+.2	.	+.1	+.2	.	.	R	+.2	.	.	.	.	.
Carex Halleriana Asso.	1.2	.	.	.	.	1.2	.	.	.	.	.	.	.	.	.	.	.	+.2	.	.	.	.	.	.
Buxus sempervirens L.	R	+°	.	1.1	2.2	2.2	.	.	.	.	.	1.2	1.3	.	.	2.1	.	.	.	.	.	2.2	2.2	2.2
Quercus coccifera L.	R	.	.	+.2	.	+.2	.	.	.	+	.	2.2	.	.	+.1	R	+	+.2	.	.	.	.	.	.
Juniperus oxycedrus L.	.	.	.	+.1	+.1	.	+	1.2	+.1	1.2	.	.	+	+	+.1	+.2	3.2	+.1	+.2	.	+	+.1	1.2	+.1
Juniperus phoenicea L.	.	.	.	+.1	+.1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhamnus alaternus L.	.	.	.	.	.	+	.	.	.	.	.	+.1	.	.	.	.	.	+.1	.	.	.	.	.	.
Dorycnium suffruticosum Villars	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+.1	.	.	+.2	.	.
Thymus vulgaris L.	+	+	+.1	.	.	.	.	+	.	+	.	+.1	.	.	.	.	+	(+)	.	+.1	.	.	.	.
Teucrium polium (L.) Ry.	+	+	+.2	R	+.1	.	+.1	2.2	+.2	+	+.2	+.2	+	.	.	.	+	+.2	.	.	.	.	+.2	.
Globularia Willkommii Nyman	.	.	1.2	+.1	.	.	.	.	+.1	.	.	.	.	.	.	.	.	.	.	.	.	1.2	+.2	+.2
Bupleurum rigidum L.	.	.	.	.	.	.	2.2	.	+.1	1.1	.	+.1	.	.	.	.	+.2	1.2	.	.	+.1	+.1	+.1	+.1
Helichrysum stoechas (L.) DC.	.	+	+.1	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Helianthemum hirtum (L.) Pers.	R	+.2	.	.	.	.	.	+	.	.	.	+.2	+	.	.	.	.	.	.	.	.	.	.	.
Argyrolobium Linnaeanum Walp.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poterium Magnolii Spach.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Chlora perfoliata L.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	1.1	+.1	.	.	.	.
Hieracium pilosella L.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Hippocrepis glauca Ten.	.	.	.	.	.	.	+	+.2	.	+	.	.	.	.	.	.	.	+.1	+.2	.	+.2	.	.	.
Ophrys araneifera (sensu lato) Huds.	+	.	.	.	.	+	+	.	.	+	1.1	+.1	R	.	+.1	.	.	.	.	+.1	+.1	.	.	.
Genista scorpius (L.) Lmk.	.	+	.	.	.	+.1	+.2	+	.	+.1°	.	+	.	.	.	.	+	+	.	+.1	.	+.1	+.1	+.1
Ononis pusilla L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1.1	1.1	.	.	.	.	.
Fumana thymifolia (L.) Verlot	.	.	.	.	.	.	.	.	.	1.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Seseli elatum (L.) Gouan	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+.1
Tortella inclinata Limpr.	+	.	1.3	1.2	.	1.2	.	.	+.2	.	1.2	+.2	2.2	.	.	.	.	.	.	.	.	+.2	+.2	.

RUBI IN THE NORTHEASTERN PART OF THE NETHERLANDS

(A floristic and vegetational study)

BY

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> "The almost inexhaustable power of nature to vary is illustrated very beautifully by this differentiation of the blackberry populations into innumerable local floras. (Å. GUSTAFSSON (1943), l.c. p. 156)

I. INTRODUCTION

There is no uniformity in the geographical distribution of the various European *Rubus* species and not only the main phyto-geographical districts but even much smaller areas appear to possess their own combinations of species. A survey of the available data has been given in 1943 by Å. GUSTAFSSON in his fine book: "The genesis of the European Blackberry Flora".

The knowledge of the distribution of the brambles within the Netherlands at that time distinctly lagged behind that of their distribution in the surrounding countries, viz. in N. W. Germany, Belgium, Great Britain and Scandinavia, where the investigations of various serious batologists already had laid a sound foundation.

In N. W. Germany the pioneer work of K. E. WEIHE and C. G. NEES VON ESENBECK (1822—1827) had been followed by the painstaking studies of W. O. FOCKE, Bremen, that were continued for more than 60 years and led to a valuable insight into the distribution of the various species. Another result of these studies was the description and classification of many species and forms that so far had been overlooked or that were unsufficiently known.

Focke's lifework has become a classic in its kind. It has laid the foundation for a more exact knowledge of the European brambles, a branch of science, in which so much amateurish work has been done that it had got into utter confusion. The number of local forms of which descriptions had been published had become enormous and the descriptions themselves were often unsatisfactory.

The singling out among the overpowering wealth of forms (Focke's "Formen-Schwärme"), of species with a larger area of distribution, was the great merit of this investigator, who may be acknowledged as the first batologist with modern views. His numerous publications appeared between the years 1868 and 1914.

For Belgium we have at our disposal a paper published by A. Charlet, L. Magnel and A. Maréchal in 1928 and for England the publications of C. C. Babington (1846, 1869), W. M. Rogers (1900), H. J. Riddelsdell (1920) and W. Watson (1946).

A survey of the Scandinavian *Rubi* (Norway, Sweden and Denmark) is given in the studies of C. E. Gustafsson (1938) and Å. Gustafsson (1943).

The most complete report on the distribution of species up to 1913 is to be found in H. Sudre's big monograph: "Rubi Europae" (1908—1913). The classification given in this standard work has in the main been followed by us.

In the Nederlandsch Kruidkundig Archief, 13 (1903) L. Vuyck gave a list of *Rubus* species that might be expected in the Netherlands or had already been collected there. This list was based on the work of Focke. In 1919 H. Heukels, in his "Flora van Nederland" gave descriptions of the species that were known at that time, and a list of these species is found also in the 11th edition of the "Geïllustreerde Schoolflora voor Nederland" by Heukels and Wachter. This list, however, is by no means complete and it contains moreover several errors.

Further may be mentioned here the notes by A. de Wever on the brambles of the southern part of the province of Limburg (1915). His specimens were revised by Focke and by Sudre.

Moreover under the heading: "Nieuwe vindplaatsen" (in: "De Levende Natuur" and in "Nederl. Kruidk. Archief" and in several other places in the latter periodical (i.a. in the excursion reports of the K.N.B.V.) the presence of various hitherto unreported *Rubi* has been mentioned. Extensive bramble collections are found in the larger herbaria in the Netherlands, in particular in the "Rijksherbarium" and in the herbarium of the K.N.B.V. at Leyden. The naming of these collections was not always satisfactory but a large part of the specimens has now been revised by us. J. H. Kern and Th. Reichgelt have started with the compilation of our knowledge of the Dutch Rubi for the "Flora Neerlandica". Much aid has been given to us by these two botanists, to whom we are truly thankful.

Our first contribution to the knowledge of the brambles of the Netherlands appeared in 1950: "De voornaamste bramen in het Drentse District"; in this publication 20 species were enumerated and discussed, and a key to these species was given.

It is our intention to continue this series of contributions with separate studies of the most important bramble centra in our country, and also with papers on other questions relating to this group of plants. They are meant as preliminary steps to a monograph of the brambles of the Netherlands. The third contribution, will give a complete survey of the brambles occurring in the phyto-geographical Drenthian district; it will also contain a number of new findings. This district has already proved to be rich in species that are rare or absent in other parts of the country.

We hope that this fourth contribution which deals not only with floristic details but also with the distribution of the species and with the part they play in various plant communities, will rouse an interest in this vast and engaging genus and its multifarious problems.

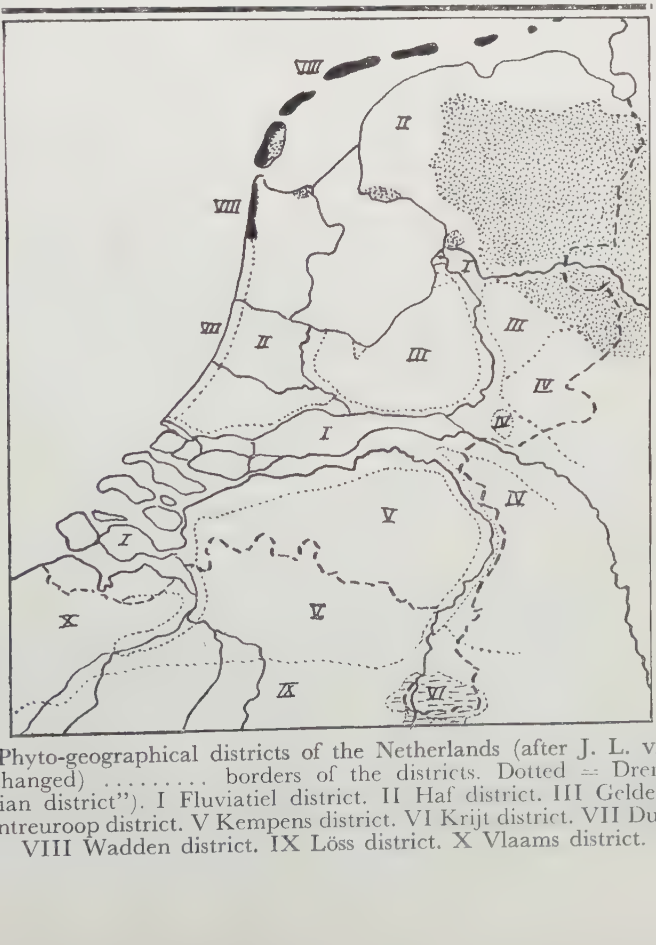

Fig. 1. Phyto-geographical districts of the Netherlands (after J. L. VAN SOEST; slightly changed) .... borders of the districts. Dotted = Drents district ("Drenthian district"). I Fluviatiel district. II Haf district. III Gelders district. IV Subsentreuroop district. V Kempens district. VI Krijt district. VII Duin district. VIII Wadden district. IX Löss district. X Vlaams district.

II. The Drenthian District

The area that forms the subject of this study extends in the east as far as the German frontier and is bordered in the N.W. and S. by an imaginary line drawn from Nieuweschans past Groningen, Dokkum, Leeuwarden, Heereveen to Dalfsen and from here eastward along the valley of the river Vecht past Marienberg to Almelo and Oldenzaal. It includes moreover Gaasterland, Vollenhove and parts of Wieringen and Texel (Fig. 1).

Characteristic for this area, which the Dutch plantgeographers call the "Drenthian District" are loamy sands resting on a slightly undulating ground moraine.

In a former period these deposits must have been covered by stagnant water; this is proved by the presence of extensive peat formations, which reach to the soil's surface, and by that of hardpans in the sands themselves. The district comprises in the first place sands and loams, marshes, moors and brook deposits, but not the clays that are here and there found transgressing its boundaries.

The surface of this weakly undulating landscape lies between ± 0 and 25 m above sea level ("N.A.P."). On the map of the stations where the bramble flora was studied (Fig. 3), the river systems have been indicated and also the provincial borders, the railway Zwolle—Groningen and the principal villages.

The Angiospermous flora of this district contains northern (boreal and montane) as well as atlantic elements.

According to H. Walter (1927) the following species belong to the firstnamed category:

Andromeda Polifolia L.
Arnica montana L.
Cornus suecica L.
Empetrum nigrum L.
Goodyera repens R. Br.
Linnaea borealis L.
Lysimachia thyrsiflora L.
Lycopodium annotinum L.
Majanthemum bifolium W. Schn.
Nardus stricta L.
Paris quadrifolia L.
Parnassia palustris L.
Phyteuma nigrum Schm.
Polygonatum verticillatum All.
Rubus saxatilis L.
Scheuchzeria palustris L.
Sparganium affine Schm.
Stellaria nemorum L.
Trientalis europaea L.
Vaccinium Myrtillus L.
Vaccinium Oxycoccus L.
Vaccinium Vitis-idaea L.

The atlantic group of species comprises:

Corydalis claviculata Lam. et DC.
Erica Tetralix L.
Galium saxatile L.
Genista anglica L.
Genista pilosa L.
Hypericum elodes L.
Ilex Aquifolium L.
Illecebrum verticillatum L.
Lobelia Dortmanna L.
Hammarbya paludosa O. Kuntze
Cicendia filiformis Delarb.
Myrica Gale L.
Narthecium ossifragum Huds.
Pedicularis sylvatica L.
Primula acaulis Grufb.
Sarothamnus scoparius Wimm.

On the whole there is a close connection with the flora of N.W. Germany; Central-European species on the other hand, are rare. Many species that are known from Germany, France and Belgium, and that are also met with in the southern part of the Netherlands are altogether absent.

In topographical respect it is noteworthy that the district shows no important differences in level, the surface sloping gradually to the N. and S.W..

The valleys formed by the brooks are shallow but often of great width. Along and within these valleys remains of the *Alnetum* and of the *Querceto-carpinetum* are still to be found; and although the extent of these rests may be very small, they often harbour a very remarkable flora and fauna.

The long-established coppice woods as well as the hedges and the often luxurious scrub along ancient country and cattle tracks, the so-called "Drentse wildgroei" may also contain rests of the original flora, i.e. of the former oak and birch woods on the higher soils. These soils are now mostly used for agricultural purposes.

Originally extensive heaths formed also an important element of this district. Since the beginning of this century these heaths have almost all been brought into cultivation, and this has caused a total change in the landscape.

Many of the earlier floral and faunistic dorados have given room to monotonous food-producing fields. May at least those parts that have been set apart as nature reserves been spared for the benefit of future generations.

A widely different element in the landscape is formed by the aeolian sands with inland dunes, low lying, wind-swept plains, cliffs, moors and pools. These areas have now for the greater part been afforested, but some plots that were considered valuable from a scenic or a biological point of view have been spared as nature reserves. The extensive peat-formations have for the greater part been drained and converted into fields.

The streams were originally strongly meandering and as their meanders constantly changed their position, there was every opportunity for the development of marshy moorland with all its floristic wealth. In the higher parts of the valleys deciduous forests, rich in species, were found. By the normalisation of the streams and the advance of agricultural practice these picturesque valley landscapes too have lost much of their original character. As relicts of the flora of the former forests, moors and catchment areas we may find here species like *Primula acaulis*, *Phyteuma nigrum*, *Anemone nemorosa*, *Anemone ranunculoides*, *Lamium Galeobdolon*, *Adoxa moschatellina*, *Chrysosplenium alterniflorum*, *Parnassia palustris* and various *Carices*.

Amongst the woody plants found in the valleys the following species are noteworthy from a phyto-geographical point of view: *Salix pentandra*, *Rhamnus cathartica*, *Euonymus europaea*, *Populus tremula*, *Corylus avellana*, sometimes *Ulmus campestris* var. *suberosa*, the cork elm and *Acer pseudoplatanus*. Less characteristic but components are a.o.: *Ilex aquifolium*, *Crataegus monogyna*, *Rosa canina*, *Viburnum Opulus*, *Prunus spinosa*, *Salix Caprea*. The following orchids are present: *Orchis Morio*, *Orchis latifolia* and *Platanthera bifolia*. They are found associated with *Caltha palustris*, *Cardamine pratensis* and *Lychnis Flos-cuculi* in boggy meadows. *Viola palustris* too is still present in large numbers. It may be said that the Drenthian District notwithstanding the deterioration of its flora belongs to those parts of the Netherlands where many species have been saved that elsewhere since long have disappeared. How far this impoverishment is reflected in the bramble flora will be discussed in the following paragraph.

The bramble-flora undoubtedly belongs like the flora of heath and moorland and of alderbogs to those that are most strongly menaced by mankind. As they are considered a nuisance, brambles during the wintermonths are regularly mowed down and burned. Heath and forest fires too have contributed to their destruction, in the first place by destroying the brambles communities themselves, but also by giving species with a stronger spreading power, a chance to occupy the vacant spaces. It is interesting to follow the result of this struggle between man and the bramble in this mosaic of landscapes.

The types of soil on which brambles are growing are of many kinds but they always possess a high content of organic material and of water. On dry sands and on purely mineral, alkaline soils brambles are generally absent and in case they do occur, their growth, as a rule, is stunted. For the rest they are found on peat, sand and loam, on forest soils rich in organic material, and on cultivated soils rich in nitrogen.

According to Focke brambles avoid those climatic regions where rainless periods are frequent.

In S. Europe with its rainless summer months *Rubus* species are much scarcer than in Central Europe. Very dry localities are generally avoided, in our own region too. This is seen in the inner dunes, the higher parts of our heaths and dry woods. But very moist localities are also avoided, even by the species that are found occasionally in catchment-areas, on stream banks and in marshy woods or that show a preference for such stations. Several *Suberecti* such as *R. Nessensis*, *R. nitidus* and *R. integribasis* belong to the latter group, but disappear as soon as the water becomes stagnant and the locality boggy. This proves that they require well aerated soils.

The humus content of the soil, in itself a function of the local saturation deficit (law of Jenny), decides whether a seedling will be able to develop to a fullgrown and vital plant. The rooting of stemtips and probably the formation of buds on the roots (as in the case of the *Suberecti*) will probably also depend for a large part upon this factor.

Further the nutritional value of the soil water is evidently of great importance. A high amount of nitrogen and a weakly acid reaction of the substrate, which means easily available nitrogen compounds are necessary for a good development.

It is therefore of little importance whether the substrate by which this combination of factors is provided. consists of loam, clay, sand or gravel, and it explains therefore the occurrence of brambles in seemingly very different surroundings. What we have to prove is that the selective influence of these environments is determined by the first-named factors.

Only when these factors have become known for a particular organism, we will be able to place the latter in its most suitable surroundings.

It is however, not a simple task to obtain such an insight, for besides the few principal factors discussed above, there are many other ones that may influence the life of the organism! The combination of all these external factors together with the idiosyncrasy of the organism itself, i.e. its vitality, adaptibility and migration power, decide the result.

It is still far beyond us to give satisfactory insight into these matters.

III. THE METHOD OF INVESTIGATION

When in 1949 we began with the exploration of the bramble flora in the vicinity of the Biological Station, Wijster, first of all a herbarium was made of specimens taken from plants that were duly marked so that they might later on, if necessary, be found back. This herbarium has formed the base for a closer investigation, floristical and ecological of the bramble flora in the Drenthian district.

The parts we collected were: 1° the typical foliage leaves, i.e. those inserted on the central part of the annual shoot (turion); and they were preferably collected during the months of July and August, sometimes a little later, the middle part of the turion was cut into pieces with a pair of secateurs, leaving one or two full-grown leaves attached to each stem fragment; 2° one to several well developed inflorescences, if possible with fresh flowers and with withered ones in order to judge the position of the sepals and the anthers during and after anthesis.

It is absolutely necessary to pay careful attention to the origin of these shoots, because we must have certainty that they are taken from the same individual. If they do not belong to the same individual, it may easily occur that two species are mixed, and this might make identification impossible. This urgent condition is not always easily fulfilled as a bramble vegetation generally is a tangle of prickly branches, often so intermixed that it is very difficult to separate one individual from another. After locality and date were noted and after the collected parts had been labelled, the latter were at once pressed. Notes on the locality, on habit, flower colour, etc. may prove useful.

To identify the species the monographs of FOCKE (1877, 1903, 1914) and SUDRE (1908—1913) were chiefly consulted. The following floras were sometimes also consulted: SCHINZ u. KELLER, Flora der Schweiz, 2nd ed., I a II (1905); LINDMAN, Svensk Fanerogam Flora, 2nd ed. (1926); BABINGTON, Manual of British Botany, 9th ed. (1904), in which to be found a survey of the British Rubi taken from

ROGERS, Handbook of British Rubi (1900), and WATSON's List of British Species of Rubus (1946).

As to nomenclature and taxonomy SUDRE's large monograph of the European Rubi has chiefly been followed, although the clear and extensive descriptions of FOCKE have also been consulted.

The study of herbarium sheets only does not enable us to recognise the species in the field. After we had identified the species, it was necessary to return to the plant from which the specimen had been taken. It is remarkable how quickly the beginning batologist learns to recognise a certain number of well distinguishable species among the much larger number of forms that are as yet unknown to him.

Encouraged by this first success he will go on, and as the number of recognizable species is gradually rising, he will gain confidence. Then the moment arrives, that it becomes more difficult, when differences of opinion arise and mistakes are made. We are now coming to the less frequent species, of which only a single group, or even a single individual is met with. Then doubt and uncertainty will arise, for one has to deal now with the vast number of local and transitional forms and hybrids. The student who wishes to master all these forms, may easily spend the rest of his life with them, for their number is endless. For practical reasons, therefore one is obliged to draw a line. Most of these minor forms and hybrids have proved to be passing appearances or perhaps recently formed species, that possess insufficient vitality or migratory power. They may be regarded as experiments in the production of new species by this more or less unstable group of plants.

For this reason this investigation has been confined to species that are more or less widely distributed, also outside the Netherlands.

After the principal species of the Drenthian district had been identified, a more detailed investigation of their distribution and their occurrence in special plant communities could follow. To this end many excursions had to be made. By way of control the vegetation records were usually taken down by both authors. Notes were made on the occupied area, on the mode of growth, on vitality and on periodicity. These records have been brought together in a simplified and more easily surveyable form in a single list. In the tables 1—3 one may see respectively:

1. A survey of the distribution of the *Rubus* species in 84 different stations within the district.
2. A survey of the occurrence of special combinations of *Rubus* species in the same stations.
3. Vegetation records of the phanerogamic flora, the *Rubi* included, in 28 of these stations.

The map (Fig. 3) show the various stations.

Besides an extensive *Rubus* herbarium, a collection of living plants belonging to the species studied by us, has been brought together. It forms the *Rubus* fruticetum of the Biological Station, Wijster. Development and periodicity of flower- and fruit-formation as well as the morphology of the plants may be studied here under practically the same ecological conditions.

Lastly seedlings have been grown from some species, to obtain an idea of the constancy of the species. This was done also by BABINGTON, ARESCHOUG and FOCKE. The last named had, already in 1877, pointed out the importance of a collection of living brambles. He himself at that time possessed in the neighbourhood of Bremen two gardens with a fair amount of European species.

IV. THE RUBUS FLORA OF THE DRENTHIAN DISTRICT

Before we begin with our survey of the *Rubus* species met with in the Drenthian district it seems desirable to explain in what way the term "species" is used by us, and what taxonomic system and nomenclature we have followed.

CARL VON LINNÉ in 1753 distinguished but two species, among the European brambles viz. *R. caesius* and *R. fruticosus*; they comprised all the European brambles that are now brought together in the section *Moriferi*. This lumping together of a large number of forms was the consequence of the artificial method of classification then in use. This method consisted in the application of a limited group of differential characters, mostly morphological ones.

Later on however, the importance of genetic factors and of geographic distribution for the delimitation of the species was gradually realized. The European bramble flora in reality comprises thousands of genetically different forms (mutually connected by transitions) each with its own area.

That LINNÉ regarded these forms as representing a single species, was a practical and altogether understandable solution.

However a more detailed study of these "forms" showed that a certain number of these were well-recognizable, and reappeared, in exactly the same way in different parts of Europe. When BABINGTON (1869), ARESCHOUG (1876), and FOCKE (1877) grew a large number of these forms from seed, it appeared that most of them were entirely or almost entirely true to type. The Linnean classification therefore had to be abandoned. FOCKE rightly remarks in his Synopsis Ruborum Germaniae (p. 24): "Es ist ein Wahn, zu glauben, dass sich alle Gruppen organischer Formen in gleichwertige Species eintheilen lassen müssen", but he added "Natürlich würde es höchst thöricht sein, wenn man nun nach der andern Seite hin fehlgreifen und das Vorhandensein von Arten überhaupt leugnen wollte". A restricted number of "species" may, after some practice, be distinguished with certainty by their habit and morphological characters.

FOCKE (1877) himself distinguished 72 of such main species or "species-complexes" for Germany and SUDRE (1913) 110 for Europe. Round these circle species certain subspecies ("micro-species" of GUSTAFSSON) and minor forms ("named varieties" of GUSTAFSSON) and their hybrids have been grouped. We are dealing here with "form swarms" which have spread across the European continent. This is shown schematically in fig. 2. Local forms, varieties and hybrids may also detach themselves in their distribution from the main species. This may happen when the new form breeds true and possesses sufficient power to multiply and to spread. In that case they become of greater importance than the numerous forms that disappear very soon or that maintain themselves with difficulty in a minor area.

Sudre (1913), distinguishes 7 categories of taxa, beginning with the main species and ending with the hybrid. Focke (1877) distinguishes five so-called "Wertstufen", and Gustafsson (1943) too accepts 5 categories, viz: "primary species", "circle species", "micro species", named variety and hybrid. We follow this last subdivision, although "primary species" probably the ancestral species, i.c. those provided with the diploid number of chromosomes, 2n = 14, are lacking in this part of the country.

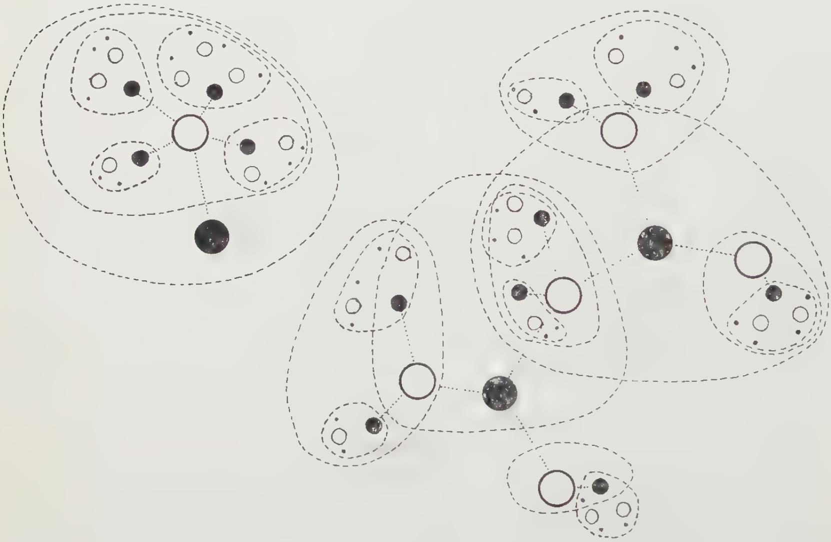

Fig. 2. Scheme of the interrelations between, and the geographic distribution of species, subspecies, varieties, forms, local strains and hybrids belonging to the european Moriferi. ● means species ("circle-species"); ○ = subspecies ("micro-species"); • = variety; ○ = local strain; · = hybrid; ---- areal boundary; .... Nearest genetic relations amongst the species, subspecies and varieties

The only representative of this group in the Netherlands is *R. ulmifolius* Schott, which grows in the southern part of the country. When the whole of Europe and N-Africa are considered, we find the following other diploid species: *R. tomentosus* Borkh., *R. canescens* DC, *R. Bollei* Focke and *R. moschus* Juz., i.e. 5 species in total.

The remaining species of which the chromosome number has been determined, are polyploids (see Gustafsson, 1943, pp. 90—93). The vast majority of the European "circle species" is tetraploid (2n = 28). Exceptions are: *R. nitidus* Wh. et N. (2n = 21), *R. candicans* Lasch

(2n = 21) and *R. Bellardii* Wh. (2n = 35); the first named and the third named species occur in our district too.

In the list following below, we have distinguished only main species ("circle species") and species ("micro species"). Local forms have not been listed. Main species have been indicated by an asterisk (*). In total 48 species are enumerated, two of which, viz. *R. saxatilis* L and *R. Idaeus* L., do not belong to the true brambles.

The numerous hybrids with *R. caesius* have been omitted, since in many cases they are difficult to distinguish and to identify, literature on this subject being scarce. Each district possesses different "*Corylifolii*", and the descriptions of these forms are either inadequate or they may be lacking altogether.

Our list of main species, subspecies and varieties in the Drenthian district is probably still incomplete. Completeness indeed can hardly be realized. The thorough exploration of a district as to its bramble flora is no simple task and would require several years.

Still, the number of main species that have already been met with (37), is larger than that reported in the literature for well explored districts of similar extent. FOCKE gives in his Synopsis the following figures:

Mecklenburg (Betke)	12 species
The Unterweser-district (Focke) . . .	20 species
Mennighüffen (Weihe)	22 species
Henneberg (Metsch)	17 species
Weissenburg (P. J. Müller)	35 species
(a district famous for its wealth of species)	
Schaffhausen (Gremli)	18 species
N-Switzerland (Gremli)	23 species

These reports date already from some time ago, and it is not improbable that since 1913 some more species have been found in these districts. However, as a top-number for floras of districts in the N.W. part of Germany FOCKE reports 40—50 species. In regard to its bramble flora the Drenthian district undoubtedly belongs to the richest parts of our country. This will be shown in Chapter VII.

Our main division of the genus into subgenera and sections is that given by FOCKE (1914), while our further subdivision into subsections, series and subseries has been based on SUDRE's "Rubi Europae" (1913). However, in our classification the position of the groups has gone down in the hierarchy by one degree, so that SUDRE's sections have become subsections, his subsections series, etc. *Moriferi* marked with an asterisk (*) correspond with SUDRE's main species and with "circle species" of GUSTAFSSON (1943). Those marked with a dot (•) are micro species with a smaller area. Where a specific epithet differring from SUDRE's Rubi Europae has been used the latter's name has been cited between brackets.

List of *Rubi* collected up to October 15th, 1951 in the N.E. part of the Netherlands.

Genus: **RUBUS** L.

Subgenus V: **CYLACTIS** Rafin.

1 * *Rubus saxatilis* L.

Subgenus X: **IDAEOBATUS** Focke

2 * *Rubus Idaeus* L.

Subgenus XII: **EUBATUS** Focke

Sectio 6: **Moriferi** Focke
A. HOMALACANTHI Dum.
Subsectio I: Suberecti P. J. Müll.

3 * *Rubus Nessensis* W. Hall (= *R. suberectus* Anders.)
4 * *Rubus fissus* Lindl.
5 * *Rubus sulcatus* Vest.
6 * *Rubus plicatus* Wh. et N.
7 • *Rubus opacus* Focke?
8 * *Rubus nitidus* Wh. et N.
9 • *Rubus integribasis* P. J. Müll.
10 * *Rubus affinis* Wh. et N.
11 * *Rubus emergens* Boul. et Malb.?
12 • *Rubus ammobius* Focke.
13 • *Rubus senticosus* Koehl.

Subsectio II: SILVATICI P. J. Müll.
Series A: *Grati* Sudre
Subseries a: *Eu-grati* Sudre

14 * *Rubus carpinifolius* Wh.
15 * *Rubus vulgaris* Wh.
16 * *Rubus gratus* Focke
17 • *Rubus sciocharis* Sudre (fa.?)
18 * *Rubus chaerophyllus* S. et S.
19 * *Rubus badius* Focke

Subseries b: *Sprengeliani* Focke

20 * *Rubus Arrhenii* J. Lange
21 * *Rubus Sprengelii* Wh.
22 * *Rubus chlorothyrsus* Focke
23 * *Rubus bracteosus* Wh. (fa.?)

Series B: *Eu-virescentes* Gen.
Subseries b: *Piletosi* Gen.

24 * *Rubus pyramidalis* Kaltenb.
25 * *Rubus macrophyllus* Wh. et N.
26 * *Rubus leucandrus* Focke (= *R. montanus* Libert; "circle species" of FOCKE) (fa.?)
27 * *Rubus Schlechtendalii* Wh.

Subseries c: *Nemorenses* Sudre

28 * *Rubus silvaticus* Wh. et N.
29 • *Rubus armoricus* Sudre
30 • *Rubus amphichlous* Sudre
31 * *Rubus egregius* Focke ("circle species" of GUSTAFSSON, 1943)

Series C: *Discoloroides* Gen.

32 * *Rubus villicaulis* Koehl.
33 * *Rubus Lindleyanus* Lees

Subsectio III: Discolores P. J. Müll
Series B: *Hedycarpi* Focke

34 * *Rubus geniculatus* Kaltenb.

Series C: *Candicantes* Focke

35 • *Rubus phyllostachys* P. J. Müll. (*R. thyrsoideus* Wimm. ssp. *phyllostachys* Sudre in Rubi europae) [1]
36 • *Rubus Leventii* Sudre

B. HETERACANTHI Dum.
Subsectio IV: Appendiculati Gen.
Series B: *Vestiti* Focke
Subseries a: *Hypoleuci* Sudre

37 * *Rubus vestitus* Wh. et N.

Subseries b: *Virescentes* Sudre

38 * *Rubus mucronifer* Sudre

Series C: *Radulae* Focke
Subseries a: *Micantes* Sudre

39 * *Rubus Radula* Wh.
40 * *Rubus Genevieri* Bor.
41 * *Rubus apiculatus* Wh.

Subseries b: *Concolores* Sudre

42 * *Rubus flexuosus* M. et Lef. (*R. foliosus* Wh. et N. ssp. *flexuosus* Sudre)

Series D: *Rudes* Sudre

43 * *Rubus rudis* Wh.

Series E: *Hystrices* Focke

44 • *Rubus horridicaulis* P. J. Müll.

Series F: *Glandulosi* P. J. Müll.

45 • *Rubus derasifolius* Sudre
46 * *Rubus Bellardii* Wh.
47 * *Rubus serpens* Wh.

Subsectio V: Caesii Focke (SUDRE: Triviales P. J. Müll.)
Grex A: *Caesii veri* Focke (1914)
48 * *Rubus caesius* L.
Grex B: *Corylifolii* Focke (1914)
(Many unidentified forms)

The way in which the species are distributed over the 4 subsections of the *Moriferi* is shown in the following table:

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[1] *R. thyrsoideus* Wimm. is a collective species, split up by SUDRE himself.

Suberecti: 11 species, of which 7 are main species and 4 are subspecies.
Silvatici: 20 species, of which 17 are main species and 3 are subspecies.
Discolores: 3 species, of which 1 is a main species and 2 are subspecies.
Appendiculati: 11 species, of which 9 are main species and 2 are subspecies.

From this it appears that the *Silvatici* are numerically by far the most important group. Still, the *Suberecti* are, at least relatively, equally well represented: this is due to the fact that in this subsection a much smaller number of species has been described.

According to GUSTAFSSON the subsections of the *Moriferi* are represented in Europe in the following way: the *Suberecti* with 7 main species, 19 subspecies and 40 named forms; the *Silvatici* with 41 main species, 160 subspecies and 316 named forms; the *Discolores* with 11 main species, 76 subspecies and 244 named forms and the *Appendiculati* by 50 main species, 440 subspecies and 1327 named forms.

It is a remarkable fact that we did not yet find a single pure *R. caesius* in our district, although several *caesius* hybrids (*Corylifolii*) proved to be present.

V. DISTRIBUTION OF THE SPECIES

Of all species and subspecies discussed here, specimens are preserved in the Rijksherbarium, Leyden, as well as in the herbarium of the Biological Station, Wijster.

First of all, some remarks will be made here on the geographical distribution of the various species in and outside the Drenthian district. The species are dealt with according to their taxonomic position.

1. **Rubus saxatilis** L Spec. p. ed. I p. 494 (1753).

Occurrence in the district: In the Netherlands exclusively known from this district, surroundings of Ter Apel, where it grows abundantly in some woods along the river Ruiten-Aa.

General distribution: S. Greenland, N. Asia, C. and N. Europe, more southwards in the mountains only. In N. Germany fairly frequent along the coast of the Baltic and of the Northsea. Further inland scarce in the plains and more frequent in the mountains.

2. **Rubus Idaeus** L. Spec. p. ed. I p. 492 (1753).

Occurrence in the district: This is the *Rubus*-species that is most widely spread in the district. It occurs in most bramble communities.
General distribution: Throughout Europe, the extreme North and South excepted. In the mediterranean region as a mountain plant only. In N. America escaped from culture and established from New England to Minnesota.

3. **Rubus Nessensis** W. Hall, Transact. Soc. Edinb. III, p. 20 (1794). (syn.: *R. suberectus* G. Anders. in Transact. Linn. Soc. XI p. 218)

Occurrence in the district: In many places, especially in woods on a soil that contains much humus and along streams. Also along roads and tracks.

General distribution: Common throughout N. and C. Europe. In Norway, Sweden, and W. Russia up to ca 60° N. Lat., eastwards as far as Moscou. Throughout Germany, particularly in the N.W. part, in Galicia, Bohemia, the Alps and N. Italy, in N. and C. France, common in England, especially in the northern part, on the other hand only locally in Scotland and Ireland.

4. **Rubus fissus** Lindl. Syn. Brit. Fl. ed. 2, p. 92 (1835).

Occurrence in the district: Fairly common on slightly acid and poor soils, even on the heath, but also in the same stations as *R. Nessensis* General distribution: In the Netherlands in the first place on the higher, sandy soils in the east and centre (Veluwe, the range of hills in the province of Utrecht, Achterhoek).

In S. Limburg, so far in one station only. In the rest of Europe along the coast of the Baltic, S. Sweden, Denmark, S. Norway, Scotland, locally in England and Ireland, Belgian Ardennes, N. Germany. From France there are as yet no records.

5. **Rubus sulcatus** Vest. in Trott. Ros. III (1828).

Occurrence in the district: estates "Oldenhof" near Vollenhove (Ov.), "Hoge Lutte" near Oldenzaal and "Lieftincksbroek" near Vlagtwedde (Gr.). Typical for humid woods. General distribution: Fairly rare in the Netherlands, the other records being the "Slangenburg" near Doetinchem, "Plasmolen" near Mook (L.), "Kloosterbos" and "Wijnandsrader Bos", both in S. Limburg. Outside our borders in Great Britain, Belgium, Germany, Switzerland, Austria and Hungary, France and N. Italy.

6. **Rubus plicatus** Wh. & N. Rub. Germ. p. 15 (1822). (syn.: *R. fruticosus* L. Spec. pl. ed. I p. 493 pro parte (1753).)

Occurrence in the district: Common along woods, borders and in scrub also along roadsides.

General distribution: In the N. German plain one of the commonest species, especially on sand and peat (Focke). Lacking east of the Kurische Nehrung. Southwards in the lower mountains and in the lower part of the Alps (Innsbruck). Seems to occur as far east as Hungary and as far south as Locarno. In Gr. Britain it becomes rarer towards the south and it is rare in Ireland. In France too it becomes rarer towards the South. Naturalized in S. Africa (var. *Bergii* Cham.) and in the mountains of Java!

7. **Rubus opacus** Focke (?) in Alpers Gef. Pflz. Stad. p. 25 (1875).

Occurrence in the district: Our finds are, so far, doubtful and restricted to two spots, at Rhebruggen and along the road Wittelte—Assen (Dr.).

General distribution: From our country there are so far but few trust-worthy records (Amersfoort, Nijmegen, Heerlen). The species is known from N.W. Germany, Belgium, France (Saône) and England (Sussex).

8. **Rubus nitidus** Wh. & N. Rub. Germ. p. 19 (1822).

Occurrence in the district: Amen and Springendal near Ootmarsum.

General distribution: Appears to occur sporadically throughout our country (N. Brabant, Gelderland). Further in N. W. Germany, Denmark, Belgium, France, Austria, Switzerland and England.

9. **Rubus integribasis** P. J. Muell. in Boulay, Ronces des Vosges 23, a. 21 (1866).

Occurrence in the district: So far from N. Drente only, where it occurs fairly frequently in several places along the streams.

General distribution: Surroundings of Nijmegen (Th. Reichgelt), N. Brabant, S. Limburg. Known from W. Germany, Belgium, N. and W. France, Portugal.

10. **Rubus affinis** Wh. & N. Rub. Germ. p. 18 (1822).

Occurrence in the district: Common, especially, along the borders and in the undergrowth of pine-plantations. Also along roadsides and in scrub.

General distribution: Known from several places in our country, also along the W. coast, a.o. at the foot of the dunes. Further: Belgium, N. W. Germany, N. and W. France and S. Sweden. Common in England.

11. **Rubus emergens** Boul. & Malb. Assoc. rub. p. 9 (1873).

Occurrence in the district: This bramble, which is considered by Sudre a subspecies of *R. affinis*, has been collected by us in several stations.

General distribution: Not yet reported from other parts of our country. In France along the lower course of the Seine.

12. **Rubus ammobius** Focke Syn. Rub. Germ. p. 118 (1877).

Occurrence in the district: Apparently still more common than *R. plicatus*, along road sides, wood borders and in scrub, also on poor sand soils.

General distribution: Especially common in the N. E. part of our country and in the "Achterhoek", also reported from Nunspeet, Loenen and Zwolle (Agnietenberg). South of our large rivers it appears to be rare. Locally in N. W. Germany, especially in Lower Saxony and Westfalia. According to C. E. Gustafsson alsoin Denmark. *R. Rogersii* Linton, may be identical with this species; it has been reported from England and is common in Scotland.

13. **Rubus senticosus** Koehl. in Wimm. & Graebn. Fl. Sil. p. 51 (1829), (syn. *R. montanus* Wirtg. Fl. Rheinprov. p. 150).

Occurrence in the district: the "Spannen" near Wijster (Dr.) and Rhebruggen (Dr.).

General distribution: Other stations in our country from where we have seen specimens are Nunspeet, Nijmegen, S. Limburg (Schinnen), the "Achterhoek" and "Twente". Further occurring in W. and C. Germany. In W. Germany northward as far as Bentheim, southward as far as Darmstadt, Silesia, Bohemen, Hungary, in the latter country especially in the mountains.

14. **Rubus carpinifolius** Wh. in Bönningh. Prodr. Fl. Monast. p. 152 (1824).

Occurrence in the district: In Drente fairly common along roads and in scrub, along woodborders and in woods.

General distribution: In the remaining parts of the country collected in S. Limburg (DE WEVER), Twente, Achterhoek and the surroundings of Nijmegen (KERN and REICHGELT). Further in Belgium, N. France, N. W. Germany, England and Tsjecho-Slovakia.

15. **Rubus vulgaris** Wh. & N. Rub. Germ. p. 38, 40 (1835).

Occurrence in the district: Amen and Ansen (Dr.) and near De Lutte (Ov.).

General distribution: N. W. Germany, Belgium, Bohemia and France. In our country from the Peel (N. Br.).

16. **Rubus gratus** Focke in Alpers Verz. Gef. Pflz. Stad. p. 26 (1875).

Occurrence in the district: Extremely common in all kinds of habitats, in cultivated land, along roads and in hedges, along wood borders and in woods, even entering the heath. A forma *laciniata* has been found in the wood of Westerbork (Dr.).

General distribution: In the Netherlands one of the most common brambles, Further in N. W. Germany and Pomerania, Denmark, Belgium, Gr. Britain and N. France.

17. **Rubus sciocharis** Sudre Bat. p. 68 (1907) (fa.?).

Occurrence in the district: a single station near Hoogeveen (Stuifzand), with pink flowers and beautiful red filaments. For the rest as in the original description.

General distribution: Not known with certainty from elsewhere in the Netherlands. Known from Denmark and Germany.

18. **Rubus chaerophyllus** Sagorski & Schultze, Deutsche Bot. Monat. XII (1894).

Occurrence in the district: This species is rare in our country. It has been reported i.a. from Neerbosch near Nijmegen (Kern and REICHGELT). The related form "fa. *brachythyrsoides* Sudre" has been collected by us at the "Lokhorst" near Amersfoort and at "Salentijn" near Nijkerk (G.), possibly also near Zuidwolde (Dr.), while "fa. *euchlooides* Sudre" was found on the "Baast" (N. Br.). The typical form occurs in Germany and Belgium, the two other forms in France.

19. **Rubus badius** Focke. Syn. Rub. Germ. p. 276 (1877).

Occurrence in the district: Common, especially in hedges and scrub, also along wood borders and in woods (Fig. 7).

General distribution: N. W. Germany, Gr. Britain.

20. **Rubus Arrhenii** J. Lange Haandb. Dansk. Fl. ed. 3, p. 386 (1864).

Occurrence in the district: In many places, but chiefly in rests of former woods and along streams (Fig. 5). At Bruntinge a turion of this species was collected with divided topleaves, i.e. with 6—7 leaflets to a leaf.

21. **Rubus Sprengelii** Wh. in Flora II, p. 18 (1819).

Occurrence in the district: Common, especially in deciduous woods, also in pine plantations. Sometimes in old coppice woods and at times even entering the heath.

General distribution: Fairly common throughout our country, but especially in the N. E. part. Common in N. Germany and Belgium.

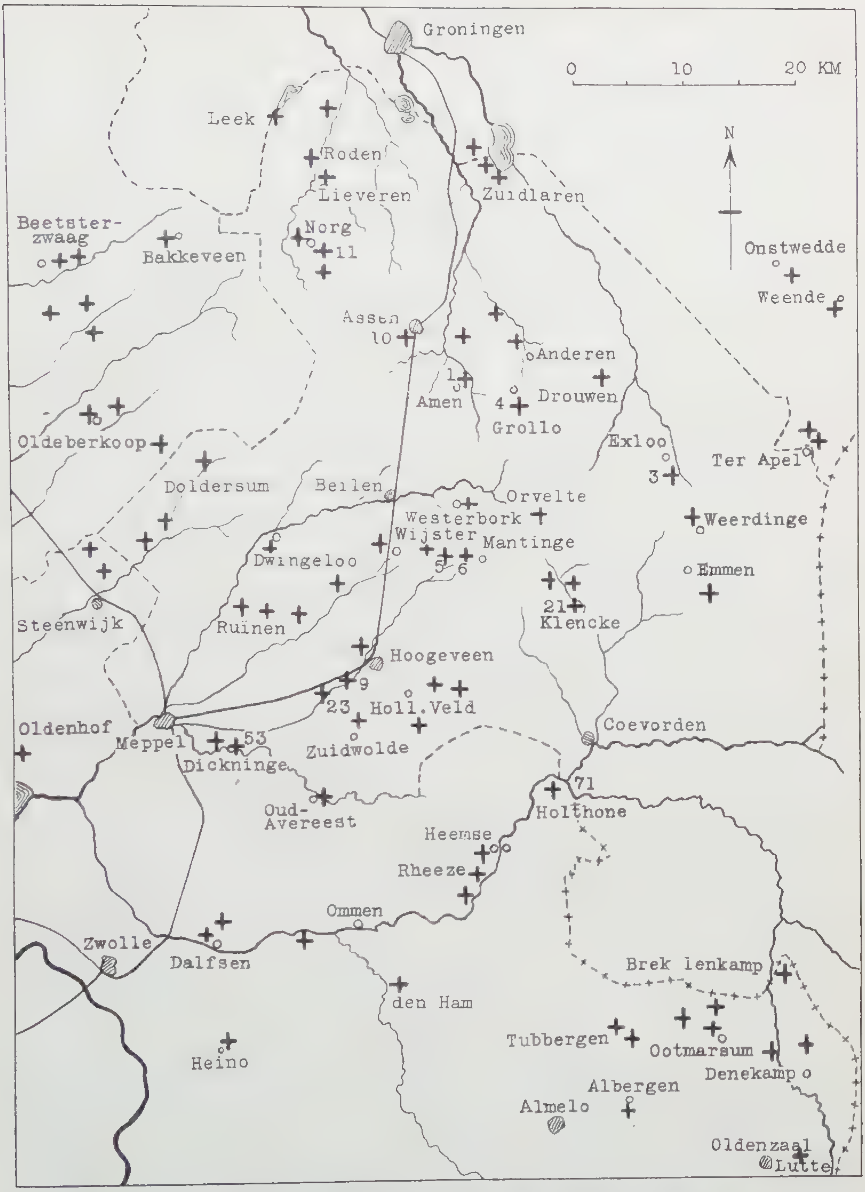

Fig. 3. Map of Drenthe. The stations where the bramble flora was studied are indicated by a cross. The figures refer to the rests of former woods mentioned in table I: 1, Amerbos; 3, Hegebos near Exlo; 4, Grolloër Holt; 5, Bruntinger Bos; 6, Mantinger Bos; 9, Kynholt; 10, Asser Bos; 11, Norger Holt; 21, De Klencke; 23, Huize Echten; 53, Dickninge; 71, De Grote Schere near Gramsbergen

From the Frische Nehrung through Germany westwards to the Rhine near Coblenz.

22. **Rubus chlorothyrsus** Focke, Abh. Nat. Ver. Bremen II, p. 462 (1871).

Occurrence in the district: Heemse (Ov.) and Hoge Lutte near Oldenzaal (Ov.).

General distribution: Collected by W. W. SCHIPPER at Slogteren (Gr.). We found the species in the former Beekbergen Forest. Otherwise unknown in our country. Further in Mecklenburg, Schleswig—Holstein, frequent in N. W. Germany and Belgium.

23. **Rubus bracteosus** Wh. ap. Lej. et Court. Comp. Fl. Belg. II p. 162 (1831) (fa.?).

Occurrence in the district: Known only from Lieveren (Dr.) in a deviating form.

General distributions: Elsewhere in our country unknown. Occurring in Gr. Britain, Belgium and Germany.

24. **Rubus pyramidalis** Kaltenb. Fl. v. Aachen. Beckens p. 275 (1845).

Occurrence in the district: common.

General distribution: Gelderland (Achterhoek, Veluwe), near Nijmegen (KERN and REICHGELT), S. Limburg etc. Also in Gr. Britain, Germany, Denmark, S. Sweden, Switzerland, Austria, C. and E. France. The area of distribution is therefore fairly large.

25. **Rubus macrophyllus** Wh. & N. Rub. Germ. p. 35 (1835).

Occurrence in the district: In the N. E. part of our country this species appears to be rather rare. Collected at Orvelte, Geesteren—Tubbergen, Albergen (Ov.).

General distribution: In our country fairly frequent i.a. in the Achterhoek and near the Hague and especially S. of the large rivers, viz. round Nijmegen, in N. Brabant and S. Limburg. Further in Belgium, Gr. Britain, Denmark, W. and S. Germany, Switzerland, Austria, C. and N. France.

26. **Rubus leucandrus** Focke (fa.?) in Alpers Verz. d. Gefpflz. Stade, p. 27 (1875).

Occurrence in the district: Wijster, Oud Avereerst and Steenbergen (near Zuidwolde, Dr.).

General distribution: N. W. Germany, southwards to the Harz and westwards to Westfalen and to the Lower Rhine, frequent round Aachen, Eupen and Malmedy, further Gr. Britain and N. France.

27. **Rubus Schlechtendalii** Weihe ap. Boenngh. Prodr. Fl. Monast. (1824) p. 152.

Occurrence in the district: By us up till now collected only at Oldenzaal (Hoge Lutte, Ov.). A specimen from Vollenhove (de Oldenhof) in the Rijksherbarium.

General distribution: Collected in the "Mastbos" near Breda, in the region of the former "Beekbergerwoud" near Apeldoorn and by KERN and REICHGELT at Beek near Nijmegen. Known from Germany (Westfalia, Minden), France, Gr. Britain.

28. **Rubus silvaticus** Wh. & N. Rub. Germ. p. 41 (1825).

Occurrence in the district: Common in woods, especially in long established ones (Fig. 4). In N. E. Overijsel apparently already less frequent.

General distribution: In our country presumably restricted to the N. E. part. Further in Schleswig-Holstein and N. W. Germany, Denmark, Gr. Britain, Austria, Bohemia, Moravia, N. and C. France and Belgium. It is therefore a species with an extensive area of distribution.

29. **Rubus armoricus** Sudre, Rubi Europae, p. 51 (1913).

To be regarded as a form of *R. silvaticus* Wh.

Occurrence in the district: In S. E. Friesland, S. of Beetsterzwaag and N. of St. Nicolaasga. In Drente along the road from ten Arlo to Echten.

General distribution: Not known to us from other localities. Occurring in France.

30. **Rubus amphichlous** Sudre, Rub. Tarn. (1909).

Occurrence in the district: Collected in some stations in S. E. Friesland and N. Drente.

General distribution: In France.

31. **Rubus egregius** Focke in Abh. Nat. Ver. Bremen, II, p. 463 (1871).

Occurrence in the district: Common, chiefly in woods (Fig. 5). Occasionally outside these woods and then mainly along streams.

General distribution: In our country further only in the Haarlemmer Hout (Haarlem). In N. W. Germany, according to Focke (1903) l.c. p. 537: "eine scharf von allen andern Brombeeren geschiedene Art", Schleswig-Holstein, Westfalia, also Schwarzwald, Belgium, Denmark, France, Austria.

32. **Rubus villicaulis** Koehl. in Wh. & N. Rub. Germ. p. 43 (1825).

Occurrence in the district: Collected in S. E. Friesland only.

General distribution: Should probably be regarded as more or less rare in our country. So far known only from the Jansberg near Mook (Reichgelt) S. Limburg (de Wever), Kotten near Winterswijk and the former "Beekbergerwoud".

33. **Rubus Lindleyanus** Lees Phyt. III, p. 361 (1838).

Occurrence in the district: Fairly common along roads and in hedges, less common in woods.

General distribution: In our country known from De Lutte near Oldenzaal, Beek near Nijmegen and the former Beekbergerwoud (G.). In Gr. Britain (frequent), N. W. Germany, along the dutch-german border (Focke) and in France.

34. **Rubus geniculatus** Kaltenb. Fl. Aach. Beckens p. 267 (1845).

Occurrence in the district: Fairly frequent in woods as well as in scrub.

General distribution: In our country known from several stations a.o.: Plasmolen, Spaubeek (S.L.), Geulle (S.L.), Ommen and Loenen, Wassenaar, Oosterbeek and Weert (N. Br.). Very common in S. Limburg. In the rest of Europe: Westfalia, Weser-area, Rhine province, Aachen, Elberfeld, Belgium and N. France.

35. **Rubus phyllostachys** P. J. Müll. in Flora, XLI, p. 133 (1858).

Occurrence in the district: Hoge Lutte near Oldenzaal (Ov.).

General distribution: Collected by us in the wood of Bekendelle near Winterswijk (G.), for the rest unknown in our country. Occurring in France, Germany, Switzerland and Belgium.

36. **Rubus Leventii** Sudre Rub. Hb. Bor. p. 34 (1902).

According to SUDRE a subspecies of *R. phyllostachys* P. J. Muell.

Occurrence in the district: den Ham (Ov.).

General distribution: Collected by us at Doetinchem, Winterswijk (G.), Doorn. (U.) and Tegelen (L.). Known from France and S. Germany.

37. **Rubus vestitus** Wh. in Bluff et Fing. Comp. Fl. germ. I p. 684 (1825).

Occurrence in the district: In Drente at Wijster only, in N. Overijsel in several localities. In hedges and along roads, also along wood borders.

General distribution: In S. Limburg one of the commonest species, also occurring round Nijmegen (KERN and REICHGELT). Further throughout C. Europe, on calcareous as well as silicious souls, Denmark, W. and S. Germany as far southwards as Vienna (Austria), Switzerland, N. and C. France, Gr. Britain, Ireland, Portugal. Is said to have been introduced in N. Sealand (ROGERS).

38. **Rubus mucronifer** Sudre Rub. Hb. Bor. p. 56 (1902).

Occurrence in the district: Although not frequent, yet found in various localities belonging to three different catchment-areas.

General distribution: Not yet known from other localities in the Netherlands. Gr. Britain, Ireland, W. France, Denmark, N. Germany, Belgium.

39. **Rubus Radula** Wh. in Boeningh. Prodr. Fl. Monast. p. 152 (1824).

Occurrence in the district: Known so far from a single but extensive area situated W. of Dalfsen (Ov.).

General distribution: In our country round Nijmegen and in S. Limburg. Denmark, Germany W. of the river Weichsel, Belgium, Austria, Hungary, N. Tirol, Switzerland (but not south of the Alps), France and Gr. Britain.

40. **Rubus Genevieri** Bor. Fl. Cent. ed. 3, II, p. 193 (1857).

Occurrence in the district: Cadoelen near Vollenhove (O.).

General distribution: The ssp. *brevistachys* Sudre collected by us in the "Liesbos" near Breda. Known from N. W. France, S. Germany and Portugal.

41. **Rubus apiculatus** Wh. in Bluff et Fingerh. Comp. Fl. Germ. I, p. 680 (1825).

Occurrence in the district: Heemse and Rheeze (O.).

General distribution: Gr. Britain, N. France, Belgium, W. Germany southwards to the Alps, Westfalia and Schleswig-Holstein, also in Switzerland, Austria, Russia (Caucasus).

42. **Rubus flexuosus** Müll. & Lef. in Poll. p. 241 (1859).

Occurrence in the district: Very frequent in woods, also in pine plantations, along wood borders and in scrub, chiefly along streams.

General distribution: In our country known from various localities i.a. Loosduinen, Vlagtwedde, S. Limburg, N. Brabant. Further occurring in Gr. Britain, Belgium, Austria, Switzerland, N. E. France, Schleswig, N. W. Germany, Rhine province, Schwarzwald.

43. **Rubus rudis** Weihe ap. Bluff et Fingerh. Comp. Fl. Germ. I, p. 687 (1825).

Occurrence in the district: In Drente only near Hoogeveen (Spaarbankbos), in Overijsel near Vollenhove (Oldenhof) and at Hoge Lutte near Oldenzaal.

General distribution: Collected by us in the Haarlemmer Hout (Haarlem), near Winterswijk and at Nijmegen; in S. Limburg frequent. Also Gr. Britain, Belgium, Germany, Switzerland, Austria, C. and N. E. France.

44. **Rubus horridicaulis** P. J. Muell. in Bonpl. p. 284 (1861).

Occurrence in the district: "Klencke" near Oosterhesselen (Dr.).

General distribution: In our country not further known. Occurring in France, Germany, Switzerland.

45. **Rubus derasifolius** Sudre in Bull. Soc. Bot. Fr. p. 334 (1905).

Occurrence in the district: Amen (Dr.), Lheebroek (Dr.) and Boyl (Fr.).

General distribution: No other localities known from the Netherlands. Found in France, Germany, Belgium, Hungary.

46. **Rubus Bellardii** Wh. in Bluff et Fingerh. Comp. Fl. germ. I, p. 688 (1825).

Occurrence in the district: Frequent in rests of former woods, rare outside the latter. Tolerates fairly deep shade, in sheltered places evergreen.

General distribution: In our country a.o. in S. Limburg (Bemelen, Houthem). Also in Germany, Denmark, S. Sweden, Gr. Britain (rare), E. France, Switzerland, Silesia, on the whole therefore with an extensive area of distribution. I.c. typical for mountain woods in C. Europe (the Alps). A very constant species, easily distinguishable by its characteristic leaf shape. Preferring moist woods, in the plain as well as in the mountains.

47. **Rubus serpens** Wh. in Lej. et Court. Compt. Fl. Belg. II, p. 172 (1821).

Occurrence in the district: Grolloër Holt near Grollo (Dr.), Echten, Exlo (Fig. 4) and Meerbos near Weerdinge (Dr.), not frequent.

General distribution: Not yet found elsewhere in our country. Occurring in Germany (Schleswig, Harz, Lausitz, Posen, Silesia), the Lesser Carpathes, throughout C. and S. E. Germany, the Belgian Ardennes, Hungary, Austria, Tirol, Switzerland, France, in the latter country chiefly in the Pyrenees, but also in Meurthe and Moselle, therefore with an extensive area of distribution. It is like the closely related *R. hirtus* W. et K. extremely rich in forms.

48. **Rubus caesius** L., Spec. pl. ed. I, 706 (1753).

Occurrence in the district: this species itself has not yet been found in the district, although it occurs along its border, viz. near Vollenhove (O.), Texel and hybrids of *R. caesius* are common in the district.

General distribution: In the Netherlands chiefly along the large rivers, in the sea dunes and on the calcareous soils of S. Limburg. Widely distributed throughout Europe and N. Asia.

VI. The plant-communities in which the rubi occur

Our survey of the bramble distribution in our district will already have made clear that many species are bound to soils that are suitable to silviculture. Below we will consider the question whether among the brambles species or groups of species are found that are more or less distinctly bound to special communities. On table III vegetational records are given of 28 stations. In most of these stations the following species are regularly met with:

Betula pubescens
Quercus Robur
Sorbus aucuparia
Ilex aquifolium
Rubus Idaeus
Rubus Nessensis
Rubus gratus
Rubus Sprengelii
Rubus egregius
Rubus flexuosus
Rubus badius
Frangula Alnus
Hedera helix
Lonicera Periclymemum
Stellaria Holostea
Corydalis claviculata
Epilobium angustifolium
Oxalis Acetosella
Maianthemum bifolium
Holcus lanatus
Polygonatum multiflorum

These elements are typical for the plant communities in oak-birch- and oak-hornbeam woods. There are many transitions between the typical representatives of these two associations and several woods in the Drenthian district belong to the latter, e.g. the habitats rich in brambles in long-established woods and in rests of former woods (Fig. 4).

It is noteworthy that the remains of well-known former woods often contain bramble-species, that are rare or lacking elsewhere in our country or are found only in localities of a similar nature. (Bruntinge, N. Lage near Mantinge (Fig. 5), near Rolde). These species, therefore, remain to a certain measure faithful to their original habitat.

Besides there are several *Rubus* species, that occur in long-established woods as well as in plantations of more recent origin, no matter whether the latter consist of conifers or of deciduous trees.

A third category of species is chiefly met with along roadsides and in fields and but rarely in woods.

In the fourth and last group we have brought together the species which have only occasionally been met with, so that a more detailed knowledge of their distribution and their connection with definite plant communities is still lacking.

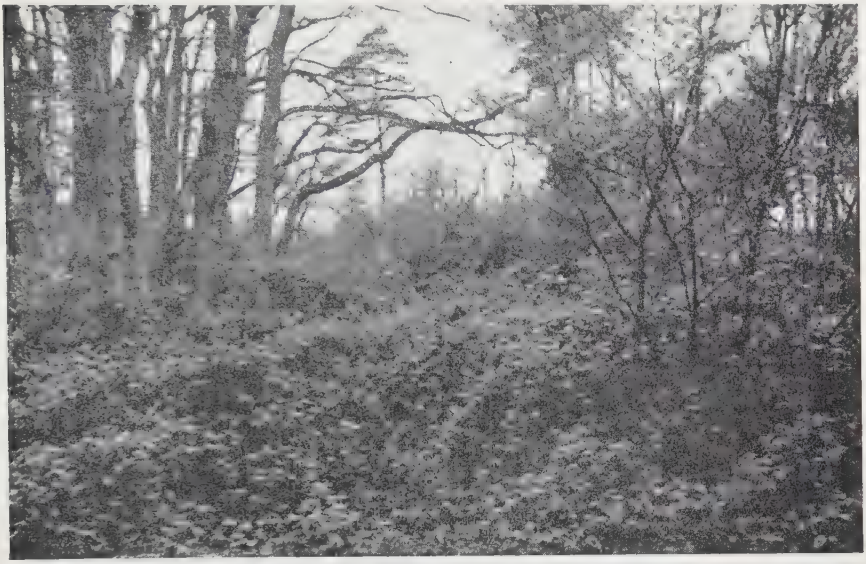

Fig. 4. Hegebos near Exloo (Dr.). Rest of a former forest with undergrowth of *R. silvaticus, R. serpens, R. Nessensis* and *R. badius*

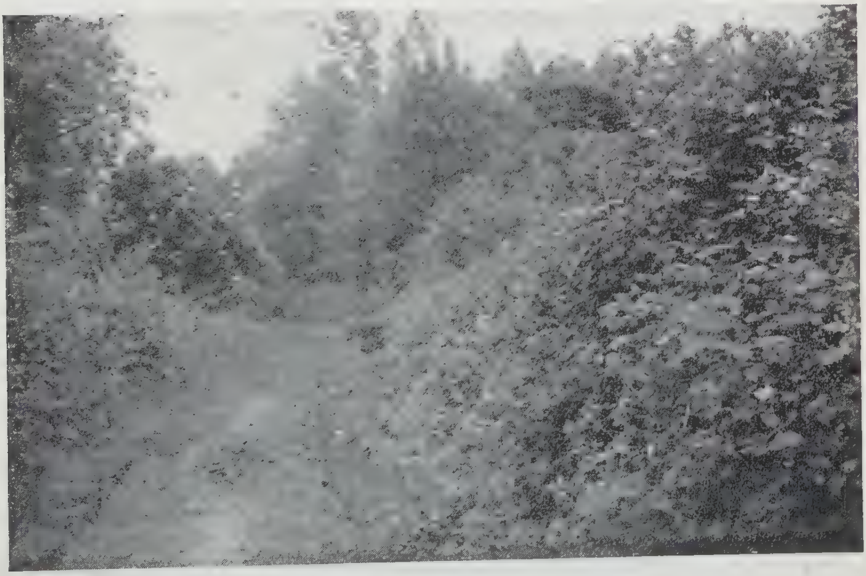

Fig. 5. Noord-Lage near Mantinge. Roadside growth with *R. plicatus, R. gratus, R. badius* and *R. Arrhenii* in a former forest

The 4 categories mentioned above are composed of the following species:

I. Species that are typical for long-established woods and for remains of such woods in the Drenthian district. (The numbering corresponds with that of the list of page 336 and that of table I):

19. *R. badius*
20. *R. Arrhenii*
28. *R. silvaticus*
31. *R. egregius*
38. *R. mucronifer*
46. *R. Bellardii*
47. *R. serpens*

II. More common species, also occurring in plantations of more recent date elsewhere in our country:

3. *R. Nessensis*
10. *R. affinis*
16. *R. gratus*
21. *R. Sprengelii*
24. *R. pyramidalis*
42. *R. flexuosus*

III. Species with their main distribution along roads and in fields, but sometimes also met with in coppice woods and in scrub and penetrating into the heath and into plantations:

4. *R. fissus*
6. *R. plicatus*
8. *R. nitidus*
9. *R. integribasis*
12. *R. ammobius*
14. *R. carpinifolius*
33. *R. Lindleyanus*

IV. Species that have only occasionally been met with and of which consequently no main distribution can be given:

7. *R. opacus* (?)
11. *R. emergens*
12. *R. senticosus*
15. *R. vulgaris*
22. *R. chlorothyrsus*
23. *R. bracteosus* (fa.?)
25. *R. macrophyllus*
26. *R. leucandrus* (fa.?)
30. *R. amphichlous*
32. *R. villicaulis*
34. *R. geniculatus*
37. *R. vestitus*
39. *R. Radula*
41. *R. apiculatus*
43. *R. rudis*
44. *R. horridicaulis*
45. *R. derasifolius*
36. *R. Leventii* a.o.

The species enumerated above recur in the 4 vertical colums of table II, where they are indicated by their numbers.

Some of the *Rubus* stations from table I have been described in detail in order to give an idea of plant communities in which the brambles occur (Table III). The map too should be consulted.

A. Examples of long-established woods and of forest remains:

1. The former forest of Amen. This has been strongly influenced by mankind (roads, woodcutting) and has now been reduced to scrub in which oak, hazel, and birch are present; borders the meadows along a stream called Amer diepje. As the vegetation

of the surrounding area was included, no clear picture of the true forest flora is obtained. Chromotop. map 1: 25000, p. 187.

3. The Hegebos, S. E. of Exloo, on the Hondsrug. This is a fairly well-preserved oakwood, ± 25 m above N.A.P. Chromotop. map 1 : 25000, p. 207 (Fig. 4).
4. The Grolloër Holt, S. of Grollo, ± 20 m above N.A.P. Oak wood, probably planted long ago on ancient forest soil. Chromotop. map 1 : 25000, p. 188.
5. The Bruntinger-Bos. Remain of a former forest along a stream, E. of the village of Bruntinge. This wood consists chiefly of oak trees and the undergrowth is rich in bracken. Moist. Chromotop. map 1 : 25000, p. 223.
6. The Mantinger Bos near Mantinge. This is said to have been known from ± 1000 A. D., according to monastery chronicles. Moist scrub with many old hollies and much bracken, also some old oak and beech trees, although mostly oak and birch. Chromotop. map 1 : 25000, p. 223 (Fig. 7).
9. The Kynholt, S. of Hoogeveen. A small rest of what in earlier times, according to the archives, must have been an extensive forest. Composed of high oak and beech trees with undergrowth a.o. of holly and hazel, and sitated along a stream called Echtener Stroompje. Poor in *Rubus* species, but characterized by the absence of the categories III and IV. Chromotop. map 1 : 25000, p. 239.
10. The Asser Bos. The southern and most ancient part of the municipal wood containing old high oaks and much undergrowth of holly and hazel; moist. Chromotop. map 1 : 25000, p. 139.
11. The Klencke, Southern part. Oak wood, already known as a wooded estate in 900 A.D. A dense undergrowth of brambles, chiefly *R. Bellardii* and *R. flexuosus*. Chromotop. map 1 : 25000, p. 241.
23. Estate of Echten. A long-established wood west of the ancient mansion; new plantations have been added. Some old specimens of hornbeam and heavy beeches. The surrounding area too has been included in the vegetation record, so that no true picture of the forest flora has been obtained. Chromotop. map 1 : 25000, p. 256.
71. The estate "Grote Schere" near Gramsbergen. Old oak wood, with an undergrowth of brambles, which though dense is rather poor in species (7). Characterized by the absence of the categories III and IV. Chromotop. map 1 : 25000, p. 275.

B. Examples of plantations, sometimes with an ancient nucleus:

18. The Sterrebos near Frederiksoord. A plantation consisting of various kinds of woody plants, sporadically with an undergrowth of brambles. Chromotop. map 1 : 25000, p. 202.
19. Pine wood, West of Wijster, planted in 1901. Now after 50 years, with a rich undergrowth of brambles. Moist, here and there loamy sand soil. Chromotop. map 1 : 25000, p. 223.

24. Near Hollandse Veld, a village east of Hoogeveen. Woods planted in the first half of the 19th century, now mostly dug up and felled. Chromotop. map 1 : 25000, p. 257.
28. Hollandse Veld, southward. High woods of *Pinus silvestris* with many brambles in the undergrowth. Chromotop. map 1 : 25000, p. 257.
32. The Eeze near Steenwijk. Mostly pine and oak, locally with many brambles. Chromotop. map 1 : 25000, p. 220.
54. Woods of Eleveld, along the Pesserdijk, S. E. of Hoogeveen. Humid pine woods with many mosses. Chromotop. map 1 : 25000, p. 240.
73. Woods east of Beetsterzwaag. Oak woods on sand soil, much scrub. Chromotop. map 1 : 25000, p. 148.

C. Examples of roadsides and fields with brambles

7. Eursinge, near Ruinen. The meadows along the stream are surrounded by scrub with an abundant growth of brambles. Chromotop. map 1 : 25000, p. 239.
47. Sandy road near Zuidwolde. Dense bramble hedge between the road and the meadows with but few other woody plants. Chromotop. map 1 : 25000, p. 256.
56. Kraloo. A wild bramble growth along a sand road bordering cornfields east of Kraloo. Chromotop. map 1 : 25000, p. 222.
68. Heemse, opposite Hardenberg. Scrub with brambles, surrounding a field; also along a sandy road. Chromotop. map 1 : 25000, p. 291.
57. Spannen, east of Wijster, Sandy road along the valley's edge, with many brambles. Chromotop. map 1 : 25000, p. 223.
76. Rome, South of Beetsterzwaag, a grassy dyke formerly used by the tramway; it accompanies the paved road leading to Gorredijk.

A less pronounced bramble flora is found in:

D. Valleys, of which the following examples are given: no 8, 41, 42, 50, 59, 60, 61, 72 and 78.

E. Shelter-belts, formed by coppice woods, with the following examples: 7, 26, 29, 30, 47.

J. HOUZEAU DE LEHAIE (1928) has drawn the attention to the part, that *Rubus* communities may play in the succession leading to forest. These communities would owe their origin to seeds dropped by birds in suitable places. When the young plants are not disturbed they grow vigorously and spread in all directions.

The bramble community, in its turn, would form a very suitable bed for the seedlings of *Cupuliferae*, which by the favourable and quick conversion of nitrogen compounds in the soil below the brambles have a good chance to succeed. When treegrowth becomes denser, the growth of the bramble community is stopped. In one special case this happened after 10 years. Subsequently it begins to shrink and in the wood just mentioned the original bramble community had

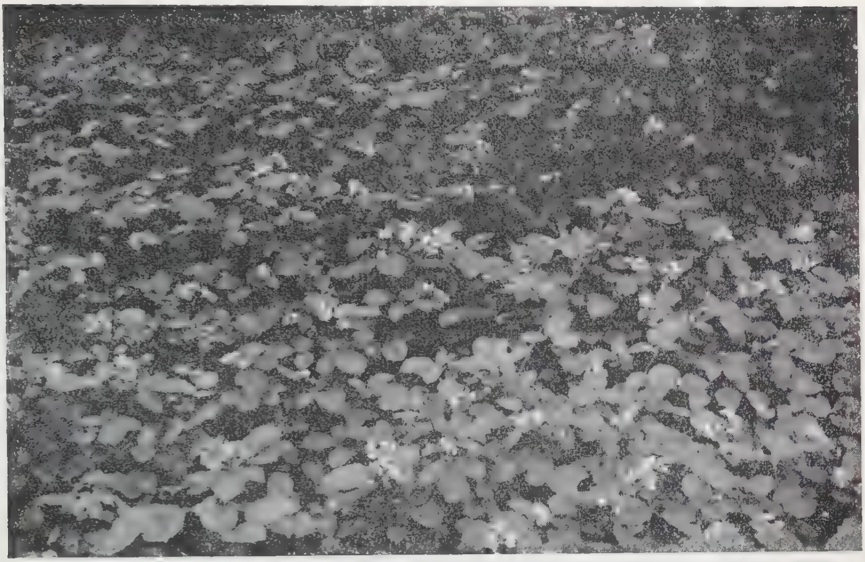

Fig. 6. Pure stand of *R. egregius* in the undergrowth of a wood at Rhebruggen

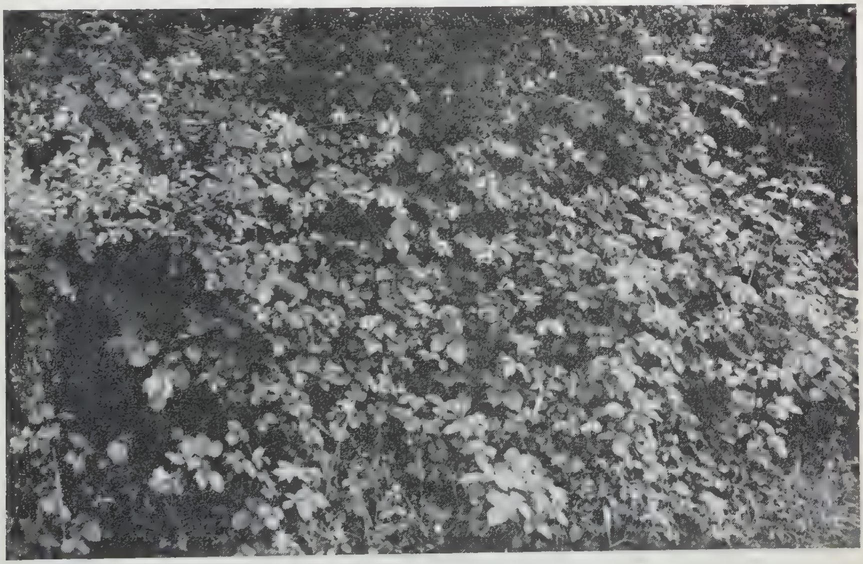

Fig. 7. Along the margin of the wood at Mantinge. *R. badius* flowering

in 30 years' time been reduced to half of its largest extension. He ends his exposition with the following pronouncement: "La place des *Rubus* dans les formations forestières est désormais accessoire. Ils doivent se confiner a la lisière des massifs d'arbres, ou dans leurs parties les moins denses".

With regard to the light requirement of the brambles Focke (1877, p. 22) remarks: "Die Lichtbedürftigkeit der verschiedenen Brombeerarten ist nicht die nämliche. Im Waldesschatten, in welchem manche *Glandulosi* üppig gedeihen und reichlich Blüthen und Früchte bringen, erhalten sich andere Arten nur kümmerlich. Im Allgemeinen ist bei den Schattenformen die Consistenz der Blätter schlaffer und der Filz der Blattunterflächen geringer, während die Sonnenformen häufig ledrige, unterseits weissfilzige Blätter haben. Indess sind nicht alle Arten in diesen Beziehungen gleich veränderlich. Manche Arten bekommen in der Sonne keine Spur von Filz, während andere (z.B. *R. bifrons*) auch im Schatten ihre weissen Unterflächen behalten. Allgemein gültige Regeln lassen sich darüber nicht aufstellen, sondern jede einzelne Art besitzt ihre besonderen Eigentümlichkeiten".

R. Tüxen (1950, pp. 165—171) reckons the *Rubus* stands to the nitrophilous weed communities of the Euro-siberian region. He includes them in the order *Epilobietalia angustifolii* (Vlieger, 1937), of the class *Epilobieta angustifolii* Tx. et Prsg. 1950, by which he means the "Schlagpflanzen-Gesellschaften" i.e. the associations that establish themselves in those parts of the woods where the trees have been felled. These associations are found in all deciduous and coniferous woods with the exception of those in the higher parts of the mountains, the alder bogs and the Betula-pubescens association on peat. They are lacking in the mediterranean-region. The species he regards as typical for this order are: *R. Idaeus* L, *Epilobium angustifolium* L. and *Calamagrostis epigeios* (L.) Roth.

The *Rubus* communities of N. W. Germany could be brought together in 2 alliances, 1° the *Lonicero-Rubion silvatici* Tx. & Neumann 1950 and 2° the *Sambucus-Salicion Capreae* Tx. & Neumann 1950. As typical species for the first alliance are given (l.c. p. 169):

R. silvaticus Wh. & N.
R. Sprengelii Wh.
R. affinis Wh. & N.
R. Schleicheri Wh. & N.
R. pyramidalis Kaltenb. a.o. *Rubi*

As differentiating species of this alliance (eventually typical species) he mentions:

Sorbus aucuparia L.
Quercus Robur L.
Betula pendula Roth.
Frangula Alnus Mill.

adding as a note:

"Sehr häufige Initial-Gesellschaft des natürlichen Waldes auf älteren Schlägen oder auf Lichtungen, besonders in Kiefern-Forsten auf den Standorten von *Quercion-roboris-sessiliflorae*-Wäldern im subatlantischen N. W. deutschen Flachland. Wahrscheinlich vielweiter verbreitet.

Die Gesellschaften dieses Verbandes sind hervorragende Verarbeiter von Rohhumus und für die Sanierung des Bodens von höchstem Wert. Lebensformen: vorwiegend Lianen "Assoziationen":

1° *Rubus gratus* — Ass. Tx. & Neumann 1950, with the regionally typical species:

R. nitidus Wh. & N.
R. gratus Focke
R. fissus Lindl.
R. pallidus Wh. & N. a.o.

Differentiating species: *Molinia coerulea* (L.) Moench. This would be the initial phase of the native *Querceto-roboris Betuletum* on silicious soil, poor in alkali of the N. W. german plain and of the lower hill districts. It occurs also in clearings in pine woods and is especially frequent in the *Querceto-roboris-Betuletum molinietosum.*

2° *Rubus silvaticus-R. sulcatus* Ass. Tx. & Neumann 1950; the regionally typical species of this association are:

R. sulcatus Vest.
R. suberectus Anders.
R. vulgaris Wh. & N.
R. hypomalacus Focke
R. Bellardii Wh.

In this association we would have the initial phase of the natural forest that develops on sandy soils with a small amount of loam or influenced by slightly alkaline soil solutions. It occurs chiefly in open spaces (clearings, enclaves) in pine woods and in slightly more eutrophic stations in the Querceto-Betuletum of the N. W. german lowland and hills.

The typical species of the second alliance i.e. the *Sambucus-Salicion Capreae* Tx. & Neumann 1950, are according to Tüxen:

Sambucus nigra L.
Salix Caprea L.
Rubus rudis Wh. & N.
R. thyrsoideus Wimm.

This would be the pioneer community of the regenerating woods in clearings in the *Fagetalia* and in the conifer plantations that have come in their stead, on hills and mountains of N. W. Germany, with further distribution in N. W. Europe.

Only two rather vaguely difined associations were to be considered here, firstly the *R. vestitus* association Tx. & Neumann 1950, which is found where the soil is loamy and the soil solution alkaline. Its only typical species is *R. vestitus* and the association is connected with the trees of the *Querceto-Carpinetum.* Secondly the *Rubus-Eubatus*-association (Oberdorfer 1938).

How far the idea that the brambles belong to the "weed" communities is right will not be discussed here. However, it is worth noting that in woods bramble vegetations are, in our experience, able to persist during a period of 30 years and more.

Since original forests, i.e. woods that are completely untouched by man, are at this moment unknown in this region, it seems rather futile to make statements on them, it is doubtless better to keep to facts.

This lines up with some remarks made by Focke in 1877, when he stated that there are many differences in behaviour between the various bramble species that occur in woods. Undoubtedly changes will occur in the flora when parts of a wood are cut down or when the trees are thinned out. The bramble flora will then, locally and temporarily, receive light and space to develop more vigorously. But even in old, dark pinewoods we may find brambles that for several decades have been growing and flourishing there. On the other hand brambles may disappear completely from a particular wood, perhaps because of the formation of acid humus or because of the drying up of the soil, but this is not in contradiction with the observation that a particular group of brambles is rather closely connected with definite forest communities. The species belonging to this group may occasionally occur outside the wood, but this happens, as a rule, only in regions with a high percentage of moisture in the air and with moist soils, rich in humus.

Besides, there are many bramble species that prefer sunny and open habitats and develop well there. When they occur in shady stations, such as woods, they are showing distinct symptoms of etiolation.

Therefore, as long as no better founded reports are obtainable on bramble communities and their connection with the surrounding vegetation, we will accept the provisional division into 4 categories mentioned above.

This should only be regarded as an attempt to obtain an idea of special methods of adaptation met with in our native brambles.

Focke already has pointed out that each species has its own demands as to its environment. The value of classifications such as that proposed above and that of Tüxen is therefore of restricted value only for our knowledge of the bramble ecology and the part the brambles are playing in the various biocönoses.

A close study of the edaphic and climatic factors in many stations, where but one species is growing (Fig. 6) may get us a little further, but in order to obtain a better founded insight experiments will have to be made.

Resuming we may say that the brambles of the categories I and II in the Drenthian district are more or less distinctly connected with the vegetation types that are known as the moist oak-birch wood (*Querceto-Betuletum-molinietosum*) and as the moist varieties of the oak-hornbeam wood (*Querceto-Carpinetum*).

The species of the *Rubi-Moriferi* that occur outside the woods cannot yet be connected with a special type of vegetation. They often occur in mosaic communities, or in transitions zones between two communities, consequently they give the impression of being rather ubiquistic. They must of course be living within the limits of their natural environment, which must be wider than those of the environment of the species that are bound to the woods. Their distribution may originally be caused by anthropogenic factors.

VII. Comparison with the Rubus flora of other phyto-geographical districts in the Netherlands

As our own experiences are mainly confined to the Drenthian district, it may seem too early to consider already at this moment the bramble flora of the other districts. Still comparisons may already be made, because we possess a report on the brambles of S. Limburg by A. DE WEVER (1915) and another one on those in the surroundings of Nijmegen. The brambles in the latter part of the country have been studied by J. H. KERN and TH. REICHGELT. We will confine ourselves therefore to a comparison between the following three districts of our country: 1° the district of Drente, 2° S. Limburg and 3° Nijmegen and surroundings. The lists below contain:

1° Species that are occurring in S. Limburg as well as in the Drenthian district:

1. *R. Nessensis* W. Hall
2. *R. fissus* Lindl.
3. *R. sulcatus* Vest.
4. *R. plicatus* Wh. et N.
5. *R. nitidus* Wh. et N.
6. *R. affinis* Wh. et N.
7. *R. senticosus* Koehl.
8. *R. carpinifolius* Wh.
9. *R. gratus* Focke
10. *R. Sprengelii* Wh.
11. *R. pyramidalis* Kaltenb.
12. *R. macrophyllus* Wh. et N.
13. *R. silvaticus* Wh. et N.
14. *R. geniculatus* Kaltenb.
15. *R. vestitus* Wh. et N.
16. *R. Radula* Wh.
17. *R. flexuosus* M. et Lef.
18. *R. rudis* Wh.
19. *R. Bellardii* Wh.
20. *R. caesius* L.

2°. Species and subspecies of the district of Drente, which have so far not been recorded from S. Limburg:

1. *R. ammobius* Focke
2. *R. integribasis* P. J. Müll.
3. *R. sciocharis* Sudre, fa.?
4. *R. chaerophyllus* S. et S.
5. *R. badius* Focke
6. *R. bracteosus* Wh., fa?
7. *R. Arrhenii* Lange
8. *R. chlorothyrsus* Focke
9. *R. leucandrus* Focke, fa?
10. *R. Schlechtendalii* Wh.
11. *R. amphichlous* Sudre
12. *R. egregius* Focke
13. *R. Genevieri* Bor.
14. *R. villicaulis* Koehl.
15. *R. Lindleyanus* Lees
16. *R. Leventii* Sudre
17. *R. mucronifer* Sudre
18. *R. derasifolius* Sudre
19. *R. serpens* Wh.

3°. Species and subspecies of S. Limburg, that have so far not been recorded from the district of Drente:

1. *R. ulmifolius* Schott
2. *R. bifrons* Vest.
3. *R. procerus* P. J. Müll.
4. *R. macrostachys* P. J. Müll.
5. *R. Muelleri* Lef.?
6. *R. micans* God.?
7. *R. glaucellus* Sudre?
8. *R. fuscus* Wh.
9. *R. insericatus* M. et Wh.
10. *R. pallidus* Wh.
11. *R. granulatus* M. et L.
12. *R. adornatus* P. J. Müll.
13. *R. Lejeunei* Wh.
14. *R. rosaceus* Wh.
15. *R. hebecarpus* P. J. Müll.
16. *R. Koehleri* Wh.
17. *R. Schleicheri* Wh.?
18. *R. humifusus* Wh.
19. *R. Kaltenbachii* Metsch
20. *R. rivularis* M. et Wh.
21. *R. incultus* Wirtg.
22. *R. biserratus* P. J. Müll.

4°. Species recorded from the surroundings of Nijmegen (KERN and REICHGELT), which have so far not been found in either of the two other districts.

1. *R. cardiophyllus* L. et M.
2. *R. polyanthemus* Lindg.
3. *R. macrothyrsus* Lange
4. *R. thyrsanthus* Focke
5. *R. Winteri* P. J. Müll.
6. *R. Muenteri* Marss.
7. *R. hypomalacus* Focke
8. *R. fusco-ater* Wh.
9. *R. anglo-saxonicus*

It stands to reason that these lists, after a more minute inspection of the districts will have to be amended.

It is also possible that the names of some species that are still uncompletely known, will have to be corrected. Still, we may already see an important difference in composition, especially when attention is paid to those species of the list (pag. 336) marked with an asterisk. They are the most characteristic species and their identification may be accepted as correct.

VIII. COMPARISON WITH THE RUBI OF THE ADJOINING PARTS OF EUROPE

After having indicated the points of difference among the bramble flora of some districts within our own country, we will now try to give an impression of the points of resemblance and of difference between our local bramble flora and that of the adjoining countries.

The Drenthian district may geologically be considered a western offshoot of the N. W. german pleistocene. It is therefore plausible to compare its brambles first of all with those of N. Germany.

Much attention has been paid to the bramble flora of the N. W. district which excells in a wealth of species.

According to FOCKE (1877) l.c. p. 31, there is a well-marked increase in the number of species when we are going from the extreme N. E. part of the former Germany (now Polen) in a western direction. In the surroundings of Kalingrad (the former Königsberg) the only species are *R. nessensis* and *R. caesius*, perhaps also *R. fissus* and an occasional *R. caesius*-hybrid. In the vicinity of the eastern border of the beech area they are joined by *R. plicatus* and *R. Bellardii.* The last named species, a pentaploid one, is widely distributed in Europe, while *R. caesius* covers a still larger area, for it is found throughout the whole of Europe with the exception of the mediterranean region and N. Scandinavia (above 58° N.L.) and in S. Siberia as far eastwards as Altai. Along the Baltic coast *R. Sprengelii* and *R. pyramidalis* (a form) are soon joining in. West of the river Weichsel according to FOCKE *R. thyrsanthus*, *R. villicaulis*, *R. Silesiacus* and *R. Radula* appear; between Oder and Elbe still more species are added, but in Schleswig-Holstein and W. of the river Elbe the wealth of species really becomes impressive. Towards the South too the number of species increases, but not towards the North. In Scandinavia the *Rubus* flora becomes poor in species and the *Moriferi* finally disappear altogether. So the further one goes westwards in Germany, the richer in species the bramble flora becomes and the more difficult therefore its study.

Along the northern slopes of the Alps and along the lower terrace of the Upper Rhine the strongest concentration of forms is to be found. The bramble flora of Lower Saxony and Westfalia shows a striking similarity with that of the Drenthian district. Nearly all the main species ("circle species") of our district are occurring there and, moreover, also those species that are rare or absent in other parts of the Netherlands, e.g. *R. Arrhenii*, *R. chlorothyrsus*, *R. egregius*, *R. mucronifer* and *R. badius*.

However striking this resemblance may be, we must realize that the same species have at least partly been found also in Denmark, England and Belgium. They may therefore be regarded as North-Atlantic species. The descriptions of the species and subspecies, that have not been recorded for N. W. Germany by Focke, 1914, are to be found in SUDRE (1913) among the "micro species" with a smaller area, e.g. *R. emergens*, *R. amphichlous*, *R. derasifolius*, *R. horridicaulis* and *R. Leventii.*

When comparing our species with the Belgian ones, a survey of which has been given by CHARLET, MAGNEL and MARÉCHAL (1928), we find a less far-going agreement. In their list we are missing: *R. ammobius*, *R. opacus*, *R. emergens*, *R. amphichlous*, *R. villicaulis*, *R. Lindleyanus*, *R. derasifolius*, *R. badius* and *R. horridicaulis*. Still a sufficient degree of similarity is present.

Among the *Moriferi* the total number of "circle species" too is much larger, viz. 86 (after GUSTAFSSON), (*Suberecti* 7, *Silvatici* 26, *Discolores* 8, *Appendiculati* 45). The most common species are *R. nessensis*, *R. sulcates*, *R. plicatus*, *R. Bertrami*, *R. carpinifolius*, *R. gratus*, *R. Sprengelii*, *R. pyramidalis*, *R. macrophyllus*, *R. ulmifolius*, *R. bifrons*, *R. geniculatus*, *R. candicans*, *R. vestitus*, *R. fissus*, *R. flexuosus*, *R. Loehri*, *R. drymophilus*, *R. rudis* and *R. Bellardii.* Remarkable is the absence of *R. villicaulis* and *R. Lindleyanus*, as these species occur in England, the latter one even very frequently and as most of our brambles are met with in Gr. Britain.

Of the main species only *R. Arrhenii*, *R. chlorothyrsus* and *R. egregius* seem to be absent and of the micro-species *R. emergens*, *R. amphichlous* and *R. horridicaulis*. All other species are present.

According to ROGERS (1900) the following 15 species are the most frequent ones in Gr. Britain: *R. Lindleyanus*, *R. polyanthemus*, *R. rhamnifolius*, *R. vestitus*, *R. dasyphyllus*, *R. mucronifer*, *R. echinatus*, *R. plicatus*, *R. Selmeri*, *R. fissus*, *R. Sprengelii*, *R. Radula*, *R. macrophyllus*, *R. Nessensis* and *R. Hystrix*. GUSTAFSSON records for Gr. Britain in total 69 circle species (*Suberecti* 6, *Silvatici* 25, *Discolores* 3 and *Appendiculati* 34).

Scandinavia has a much smaller number of brambles. C. E. GUSTAFSSON (1938) enumerates in his survey for Norway only 9 *Moriferi*, viz. *R. nessensis*, *R. fissus*, *R. plicatus*, *R. sulcatus*, *R. Selmeri*, *R. confinus* (= *R. insularis f. confinus*), *R. thyrsanthus*, *R. Lindebergii* and *R. Radula*. Moreover, there are several *Caesii*. Of these 9 species of the *Moriferi* 5 belong to the *Suberecti*, 3 to the *Silvatici* and 1 to the *Appendiculati*.

Sweden possesses 22 species (*Suberecti* 6, *Silvatici* 7, *Discolores* 2 and *Appendiculati* 7). From Denmark 34 circle species of the *Moriferi* are known, viz. *Suberecti* 6, *Silvatici* 13, *Discolores* 2 and *Appendiculati* 13.

This summary gives an idea of the character of our dutch bramble flora in comparison with that of the surrounding countries. The bramble flora of the Drenthian district shows by far the greatest similarity with that of the adjoining part of N.W. Germany, but contains at the same time some typical N. Atlantic elements, e.g. a relatively large number of *Suberecti* and *Silvatici*, but only a few *Discolores* and *Glandulosi*. The further South one comes, and the more one approaches the Pyrenees, Alps and Carpathes, the larger the number of *Discolores* and *Appendiculati* becomes, while the *Suberecti* are decreasing. The populations occurring there are vastly different, the diploid ancestral species and their nearest and more fertile allies serving as a centre. They are to be regarded as species that in refugia not covered by the mountains' ice-caps have survived the climate of the last glacial period. Since a great part of these mountain slopes have become ice-free, the surviving brambles have gradually immigrated into this new area, and have at the same time produced new forms. According to Gams (1933) new plant species would originate during the periods that new areas, become inhabitable. During the post-glacial period this happened in the southern part of the valleys, but further northward when the latter became flatter and wider, different topographical conditions arose, and here consequently different populations would have developed. The wealth of forms of C. Europe slowly decreases towards the North; the cold-resistent group of the *Suberecti* and the species *R. Bellardii*, *R. serpens* and *R. caesius* are the only ones that penetrated further northwards and here produced a number of hybrids with *R. caesius* (*Corylifolii*).

The northern climate and also the shortness of the ice-free period after the country was opened by the retirement of the Fenno-Scandinavian ice-cap, are probably the cause of the poorness of the bramble flora.

Our own country, the British islands and N. W. Germany owe their rich bramble flora to the milder climate, which is due to the nearness of the North Sea. The production of hybrids that by pseudogamic seed-formation or other kinds of apomixis are able to multiply, and the appearance of mutations will have been the cause of the great richness in forms observed in the W. european *Moriferi*. They give the impression of a strongly evolutive group of plants, and for that reason deserve our full attention.

SUMMARY

1°. Our study of the *Rubus* flora of the N. E. part of the Netherlands (Drenthian district) so far has led to the recognition of 46 *Moriferi*

of which 35 are to be regarded as circle-species and 11 as micro-species. The list on p. 12*b* includes besides the *Moriferi R. saxatilis* L. and *R. Idaeus* L. *R. caesius* L., the typical dewberry itself, however, has not yet been found. Our 46 *Moriferi* belong to 4 different subsections: 11 species, viz. 7 circle-species and 4 micro-species to the *Suberecti*. 20 species, viz. 17 circle-species and 3 micro-species to the *Silvatici*, 3 species, viz. 1 circle-species and 2 micro-species to the *Discolores*, 11 species, viz. 9 circle-species and 2 micro-species to the *Appendiculati*.

2°. The 3 tables give the following data:

I. The presence or absence of our 48 species in the stations, that have been studied by us, the number of species in each station (below) and the number of times that each species has been met with (on the right).

II. The classification of the *Rubus* species into 4 groups: 1° species that are typical for forestremains; 2° species that occur in all kinds of wood; 3° species found along road sides and in fields; 4° species so rarely met with, that their habitat is insufficiently known.

III. Vegetational records of 28 woods in which brambles were observed.

3°. On pp 15—42 the distribution of our 48 species and subspecies in and outside the area is discussed.

4°. The following species, all typical for the remains of former forests, occur also in the adjoining part of N. W. Germany but have not or only rarely been found elsewhere in our country: *R. Arrhenii*, *R. silvaticus*, *R. egregius*, *R. mucronifer*, *R. badius*, *R. Bellardii* and *R. serpens*. Common in woods are: *R. Nessensis*, *R. affinis*, *R. gratus*, *R. Sprengelii*, *R. pyramidalis* and *R. flexuosus*. Species chiefly found along roads and in fields are: *R. fissus*, *R. plicatus*, *R. nitidus*, *R. integribasis*, *R. ammobius*, *R. carpinifolius* and *R. Lindleyanus*.

5°. The two first-named groups of species are more or less distinctly associated with the *Querceto—Betuletum—molinietosum* and the more humid varieties of the *Querceto—Carpinetum*. The species from road sides and fields are not restricted to clear-cut communities, but occur also in mosaic communities and in transitional zones.

6°. The *Rubus* flora of the Drenthian district has been compared with that of the Southern part of the province of Limburg and that of the environs of Nijmegen, as far as this for the moment was possible.

7°. In conclusion the *Rubus* flora of the Drenthian district has been compared with that of the surrounding countries. It appears to be most closely related to that of N. W. part of Germany, but it contains also several N. Atlantic elements and in this respect it shows an approximation to the belgian, british and scandinavian bramble floras.

REFERENCES

BABINGTON, C. C. and H. GROVES, a. *J.* (1904). Manual of British Botany. — London

BEIJERINCK, W. en A. J. TER PELKWIJK, (1950). De voornaamste bramen in het Drentse District. — De Lev. Natuur, jrg. 53.

CHARLET, A., L. MAGNEL et A. MARÉCHAL, (1928). Contribution à l'étude de la dispersion des Rubus en Belgique. — Bull. Soc. Roy. Bot. Belg. *61.*
FOCKE, W. O. (1877). Synopsis Ruborum Germaniae. — Bremen.
FOCKE, W. O. (1903). Rubus in: Ascherson, P. und Graebner, P. Synopsis der mitteleuropäischen Flora. VI: 1. — Leipzig.
FOCKE, W. O. (1914). Species Ruborum III. — Stuttgart.
GUSTAFSSON, C. E. (1938). Skandinaviens Rubus-flora. — Bot. Not. Lund.
GUSTAFSSON, A. (1943). The Genesis of the European Blackberry Flora. — Lunds Univ. Arsskrift. N. F. Avd. 2, Bd 39, Nr 6.
HEUKELS, H. en W. H. WACHTER (1934). Geïllustreerde Schoolflora voor Nederland. 11e dr. — Groningen.
SCHINZ, H. und R. KELLER (1905). Flora der Schweiz. 2e Aufl. — Zürich.
LINDMAN, C. A. M. (1926). Svensk Fanerogamflora. 2e dr. — Stockholm.
RIDDELSDELL, H. J. (1920). British Rubi, 1900—1920. — Journ. of Bot. *58.*
ROGERS, W. M. (1900). Handbook of British Rubi. — London.
SUDRE, H. (1908—1913). Rubi Europae. — Paris.
WATSON, W. (1946). List of British species of Rubus — Journ. of Ecology, Vol. 33.
WEIHE, K. E. et NEES VON ESENBECK, C. G. (1822—1827). Rubi Germanici. — Elberfeld.
WEVER, A. DE (1915). Rubus in: Lijst van wildgroeiende en eenige gekweekte planten in Z.-Limburg. — Jaarboek 1915 v. h. Natuurhistorisch Genootschap in Limburg. — Maastricht.

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Correction. Wherever the name Rubus apiculatus Wh. is used, read: *Rubus spinulifer* M. & Lef., a subspecies of *R. Koehleri* Wh.

TABLE I

Survey of the distribution of 43 Rubus species in 84 stations in the Drenthian District

	STATIONS: RUBUS SPECIES:	Amer-Bos	Anderen	Hegebos near Exloo	Grolloër-Holt	Bruntinger Bos	Mantinger Bos	Eursinge, gem. Ruinen	Oude Diepje near Hoogeveen	Kynholt-Bos	Asser-Bos	Norger-Holt	Ter Apel (Tempelbos)	Tonckens-Bos near Norg	Aalden	Weerdinger Meerbos	Roelage-Bos near Ter Apel	Angelsloo	Frederiksoord, Sterbos	Wijster. W.	De Klencke. N.	De Klencke. S.
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	R. saxatilis L.	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–	×	–	–	–	–	–
2	R. idaeus L.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
3	R. Nessensis W. Hall	×	–	×	×	×	×	–	×	×	×	×	×	×	×	×	×	×	–	–	×	×
4	R. fissus Lindl.	–	–	–	–	×	×	–	×	–	–	–	×	–	–	–	×	–	×	×	–	–
6	R. plicatus Wh. et N.	×	–	×	–	–	–	×	–	–	–	–	×	–	–	–	–	–	–	×	–	–
7	R. opacus Focke?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
8	R. nitidus Wh. et N.	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
9	R. integribasis P. J. Müll.	×	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–
10	R. affinis Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	×	–	–	×	×	–	×	×	×	×
11	R. emergens Boul. et Malb.?	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
12	R. ammobius Focke	–	–	–	–	–	–	×	–	–	–	–	×	–	×	–	–	–	–	×	–	–
13	R. senticosus Koehl.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
14	R. carpinifolius Wh.	×	–	×	–	–	×	×	×	–	×	–	–	×	×	–	–	–	–	×	–	–
15	R. vulgaris Wh.	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
16	R. gratus Focke	×	×	×	–	×	–	×	×	–	–	–	×	–	×	×	×	–	×	×	×	×
17	R. sciocharis Sudre (fa.?)	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–
18	R. chaerophyllus S. et S.	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
19	R. badius Focke	×	–	×	×	×	×	×	×	×	×	–	×	–	–	–	×	–	×	×	–	×
20	R. Arrhenii J. Lange	×	–	–	–	×	×	–	–	–	–	×	–	×	–	–	×	–	–	–	–	–
21	R. Sprengelii Wh.	×	–	×	×	×	×	–	×	×	×	–	×	×	–	×	–	–	×	×	–	×
22	R. chlorothyrsus Focke	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
23	R. bracteosus Wh. (fa.?)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
24	R. pyramidalis Kaltenb.	×	–	×	×	×	×	–	×	–	–	–	×	–	×	×	–	–	–	×	×	×
25	R. macrophyllus Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
26	R. leucandrus Focke	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×	–	–
28	R. silvaticus Wh. et N.	×	×	×	×	×	×	–	–	–	×	–	×	–	×	×	×	×	–	–	×	–
29	R. armoricus Sudre	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
30	R. amphichlous Sudre	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
31	R. egregius Focke	×	–	–	×	×	×	–	–	×	×	×	×	×	–	–	–	–	×	–	–	–
32	R. villicaulis Koehl.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
33	R. Lindleyanus Lees	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	×	–	–
34	R. geniculatus Kaltenb.	×	×	–	–	–	–	×	–	–	–	–	–	–	×	×	–	–	–	–	–	–
36	R. Leventii Sudre	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
37	R. vestitus Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×	–	–
38	R. mucronifer Sudre	×	–	–	–	×	×	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–
39	R. Radula Wh.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
41	R. apiculatus Wh.?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
42	R. flexuosus M. et L.	×	–	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
43	R. rudis Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
44	R. horridicaulis P. J. Müll?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×	–
45	R. derasifolius Sudre	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
46	R. Bellardii Wh.	×	×	–	×	×	×	–	–	–	×	×	–	×	–	–	–	–	–	–	–	×
47	R. serpens Wh.	–	–	×	×	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–
	Numbers of the stations	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
	Total number of species	20	5	11	11	13	13	8	12	6	9	7	14	8	9	10	10	4	8	14	8	9

	STATIONS: RUBUS SPECIES:	Spaarbankbos n. Hoogeveen	Echten	Hollandse Veld, I	Hollandse Veld, II	Dwingeloo, Oldengaerde	Westerborker-Bos	Hollandse Veld, III	Hamveld n. Bruntinge	Westervelde	Zweeloo	De Eeze n. Steenwijk	Huis ter Heide n. Norg	Lieveren	Roden, Kymmell-Bos	Foxwolde	Nienoord n. De Leek	Zuidlaren, Laarwoud	Midlaren	Noordlaarder-Bos	Anderse Diepje	Looner Diepje
		22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
1	R. saxatilis L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	R. idaeus L.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
3	R. Nessensis W. Hall	–	×	–	–	×	×	×	–	×	×	×	×	×	×	–	–	–	–	×	×	–
4	R. fissus Lindl.	×	×	×	–	–	×	×	–	–	–	×	–	×	–	–	–	–	×	–	–	–
6	R. plicatus Wh. et N.	×	×	×	–	–	–	×	×	–	×	×	–	×	×	–	–	–	–	–	×	–
7	R. opacus Focke?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
8	R. nitidus Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
9	R. integribasis P. J. Müll.	–	–	–	–	–	–	–	–	×	–	–	–	×	×	×	×	–	–	–	–	–
10	R. affinis Wh. et N.	×	×	×	–	–	×	–	×	×	–	–	×	–	–	–	×	×	–	–	×	–
11	R. emergens Boul. et Malb.?	–	–	×	×	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
12	R. ammobius Focke	×	–	×	–	×	×	–	×	×	×	–	–	×	×	×	–	–	–	×	–	×
13	R. senticosus Koehl.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
14	R. carpinifolius Wh.	–	×	×	–	×	×	×	–	×	×	–	×	×	×	×	–	–	×	×	×	–
15	R. vulgaris Wh.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
16	R. gratus Focke	×	×	×	–	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
17	R. sciocharis Sudre (fa.?)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
18	R. chaerophyllus S. et S.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
19	R. badius Focke	×	×	–	–	×	×	–	–	–	–	×	×	–	–	–	×	–	–	–	–	–
20	R. Arrhenii J. Lange	–	–	–	–	–	×	–	–	–	×	–	×	×	×	–	–	–	–	–	–	–
21	R. Sprengelii Wh.	×	×	×	×	×	×	×	–	×	–	×	×	–	×	×	×	×	×	–	–	–
22	R. chlorothyrsus Focke	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
23	R. bracteosus Wh. (fa.?)	–	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–
24	R. pyramidalis Kaltenb.	–	×	–	–	–	–	–	–	×	–	×	×	–	×	×	–	–	×	×	–	–
25	R. macrophyllus Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
26	R. leucandrus Focke	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
28	R. silvaticus Wh. et N.	–	×	–	–	×	×	–	–	×	×	–	–	–	×	–	×	–	×	–	×	–
29	R. armoricus Sudre	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
30	R. amphichlous Sudre	–	–	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–
31	R. egregius Focke	×	×	×	×	×	–	–	–	×	–	×	×	×	–	×	–	–	×	–	–	–
32	R. villicaulis Koehl.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
33	R. Lindleyanus Lees	–	–	–	–	–	–	–	–	–	–	×	–	–	–	×	–	–	×	–	–	×
34	R. geniculatus Kaltenb.	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	×
36	R. Leventii Sudre	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
37	R. vestitus Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
38	R. mucronifer Sudre	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–
39	R. Radula Wh.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
41	R. apiculatus Wh.?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
42	R. flexuosus M. et L.	×	×	×	×	–	–	×	×	–	×	×	–	×	×	–	–	×	–	–	–	–
43	R. rudis Wh. et N.	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
44	R. horridicaulis P. J. Müll?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
45	R. derasifolius Sudre	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
46	R. Bellardii Wh.	×	×	–	–	–	–	–	×	–	–	–	×	–	–	–	–	–	–	–	–	–
47	R. serpens Wh.	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Numbers of the stations	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
	Total number of species	12	15	11	5	9	12	8	8	11	9	12	11	12	13	9	7	5	9	6	7	5

	STATIONS: RUBUS SPECIES:	Roden-Peize	Drijber	Lheebroek	Ruinen. N.	S. of Ansen	Rhebruggen	Doldersum	Havikshorst n. Meppel	Tiendeveen	Zuidwolde	Dickninge n. De Wijk	Eleveld-Bos n. Hoogeveen	Westerholt n. Orvelte	Kraloo-Ruinen	Spannen, E. of Wijster	Dalfsen	Den Ham	Ootmarsum	Springendal n. Ootmarsum	Geesteren	Tubbergen
		43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
1	R. saxatilis L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	R. idaeus L.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
3	R. Nessensis W. Hall	–	×	–	–	×	×	×	×	–	–	×	–	×	×	–	×	–	–	×	×	×
4	R. fissus Lindl.	–	×	×	×	×	×	–	×	–	–	×	–	–	–	–	–	–	–	–	×	–
6	R. plicatus Wh. et N.	–	–	×	×	×	×	×	×	×	×	–	–	×	–	×	×	×	×	×	×	–
7	R. opacus Focke?	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
8	R. nitidus Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×	–	–
9	R. integribasis P. J. Müll.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
10	R. affinis Wh. et N.	–	–	×	×	×	–	×	×	×	×	×	×	–	×	–	–	×	–	×	–	×
11	R. emergens Boul. et Malb.?	–	–	–	–	–	–	×	–	–	×	–	–	–	×	–	–	–	–	–	–	–
12	R. ammobius Focke	–	–	×	×	×	×	×	×	×	×	–	–	×	×	×	×	×	–	×	×	×
13	R. senticosus Koehl.	–	–	–	–	–	×	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–
14	R. carpinifolius Wh.	×	–	×	×	×	×	×	–	–	×	–	×	×	×	×	–	–	–	–	×	–
15	R. vulgaris Wh.	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
16	R. gratus Focke	×	–	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	–	×	×	×
17	R. sciocharis Sudre (fa.?)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
18	R. chaerophyllus S. et S.	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–
19	R. badius Focke	–	×	×	×	–	×	–	×	×	×	×	×	×	×	–	–	–	–	–	–	–
20	R. Arrhenii J. Lange	×	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–
21	R. Sprengelii Wh.	–	–	×	–	–	–	×	×	×	–	×	×	–	×	×	–	–	–	–	–	–
22	R. chlorothyrsus Focke	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
23	R. bracteosus Wh. (fa.?)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
24	R. pyramidalis Kaltenb.	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	×	×	–	–	–
25	R. macrophyllus Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–	×	–	–	×	×
26	R. leucandrus Focke	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–
28	R. silvaticus Wh. et N.	–	×	×	–	–	×	×	–	–	–	–	–	–	–	–	–	–	–	–	×	×
29	R. armoricus Sudre	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–
30	R. amphichlous Sudre	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
31	R. egregius Focke	–	×	×	–	–	×	×	×	×	–	×	–	–	–	–	–	–	–	–	–	–
32	R. villicaulis Koehl.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
33	R. Lindleyanus Lees	×	–	–	–	–	–	×	×	–	–	–	–	–	×	–	–	–	×	×	–	×
34	R. geniculatus Kaltenb.	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	×	–	–	–	–
36	R. Leventii Sudre	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–
37	R. vestitus Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–
38	R. mucronifer Sudre	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
39	R. Radula Wh.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–
41	R. apiculatus Wh.?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
42	R. flexuosus M. et L.	–	–	–	–	–	–	–	×	×	–	×	×	×	–	–	–	–	–	×	×	–
43	R. rudis Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
44	R. horridicaulis P. J. Müll?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
45	R. derasifolius Sudre	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
46	R. Bellardii Wh.	–	–	–	–	–	–	–	–	×	–	×	–	–	–	–	–	–	–	–	–	–
47	R. serpens Wh.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Numbers of the stations	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
	Total number of species	5	6	12	8	9	12	12	14	10	11	10	7	10	10	7	6	9	5	9	10	8

	STATIONS: RUBUS SPECIES:	Vasse	Denekamp. N.	Tilligte-Denekamp	Breklenkamp	Heemse	Rheeze	Holthone	De Grote Scheere	Oud-Avereest	Beetsterzwaag, E.	Beetsterzwaag-Olterterp	Heidhuizen	Koningsdiep, S. of Beetsterzwaag	Driehoek	Oldeberkoop	Molenbos, Oldeberkoop	Road t. Makkinga	Bekhofschans	Lindevallei I	Lindevallei II	Road t. Hemrik	Numbers of the species	Number of observations
		64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84		
1	R. saxatilis L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2
2	R. idaeus L.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	–	×	×	×	2	83
3	R. Nessensis W. Hall	–	–	–	×	×	–	×	–	×	×	–	–	–	×	×	×	×	–	×	×	×	3	53
4	R. fissus Lindl.	–	–	×	–	×	–	–	–	–	–	–	–	–	–	–	×	–	–	–	×	–	4	27
6	R. plicatus Wh. et N.	×	–	×	×	–	–	×	–	–	–	–	–	×	×	×	–	–	–	×	×	–	6	39
7	R. opacus Focke?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	1
8	R. nitidus Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	2
9	R. integribasis P. J. Müll.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9	7
10	R. affinis Wh. et N.	×	×	–	×	×	–	×	×	×	–	–	×	–	–	–	–	–	–	–	–	–	10	38
11	R. emergens Boul. et Malb.?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11	7
12	R. ammobius Focke	–	×	×	×	×	–	×	–	×	×	×	×	×	–	–	–	–	–	–	×	–	12	43
13	R. senticosus Koehl.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13	2
14	R. carpinifolius Wh.	–	×	–	×	×	×	–	–	–	–	×	×	×	–	–	–	–	–	–	×	–	14	43
15	R. vulgaris Wh.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	15	2
16	R. gratus Focke	×	–	×	×	×	×	×	×	×	×	×	×	×	×	×	×	–	–	×	–	–	16	69
17	R. sciocharis Sudre (fa.?)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	17	1
18	R. chaerophyllus S. et S.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	18	2
19	R. badius Focke	–	–	–	–	×	–	–	×	–	×	–	–	–	–	×	×	×	×	×	×	×	19	42
20	R. Arrhenii J. Lange	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20	13
21	R. Sprengelii Wh.	–	–	×	×	–	–	–	–	–	×	×	×	–	×	–	×	×	×	×	×	–	21	48
22	R. chlorothyrsus Focke	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	1
23	R. bracteosus Wh. (fa.?)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	23	1
24	R. pyramidalis Kaltenb.	–	×	×	×	×	×	×	×	–	–	×	×	–	–	×	×	×	–	–	×	–	24	36
25	R. macrophyllus Wh. et N.	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	25	5
26	R. leucandrus Focke	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–	26	3
28	R. silvaticus Wh. et N.	×	–	–	×	–	–	–	–	×	–	–	×	–	–	–	–	–	–	–	×	×	28	34
29	R. armoricus Sudre	–	–	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	29	2
30	R. amphichlous Sudre	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	30	2
31	R. egregius Focke	–	–	–	–	–	–	–	–	–	–	×	×	–	–	–	×	×	–	–	×	×	31	34
32	R. villicaulis Koehl.	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	32	1
33	R. Lindleyanus Lees	×	–	×	×	×	×	×	–	–	–	–	–	×	–	–	–	–	–	–	–	–	33	20
34	R. geniculatus Kaltenb.	–	–	–	–	×	–	–	–	×	–	–	–	–	–	–	–	×	×	–	–	–	34	13
36	R. Leventii Sudre	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	36	1
37	R. vestitus Wh. et N.	×	–	–	×	×	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	37	6
38	R. mucronifer Sudre	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×	–	38	6
39	R. Radula Wh.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	39	1
41	R. apiculatus Wh.?	–	–	–	×	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	41	2
42	R. flexuosus M. et L.	–	–	–	–	–	–	×	×	–	×	–	–	–	–	–	×	×	×	–	×	×	42	46
43	R. rudis Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	43	1
44	R. horridicaulis P. J. Müll?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	44	1
45	R. derasifolius Sudre	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	45	2
46	R. Bellardii Wh.	–	–	–	–	–	–	–	×	–	–	×	–	–	–	–	×	–	–	–	–	–	46	18
47	R. serpens Wh.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	47	4
	Numbers of the stations	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84		
	Total number of species	7	5	8	13	14	6	10	7	8	7	9	10	6	6	6	10	8	4	6	13	6		

TABLE II

Classification of the Moriferi from 84 stations in the Drenthian District into 4 categories. (The numbers in the columns correspond with those of the list of species and with those of table I)

	CATEGORIES: / STATIONS:	I Species: 19, 20, 28, 31, 38, 46, 47	II Species: 3, 10, 16, 21, 24, 42	III Species: 4, 6, 8, 9, 12, 14, 33	IV Remaining species
1	Amer-Bos	19, 20, 28, 31, 38, 46, 47	3, 16, 21, 24, 42	6, 8, 9, 14	11, 15, 34, 45
2	Anderen	28, 46	16		34
3	Hegebos	19, 28, 47	3, 16, 21, 24, 42	6, 14	—
4	Grolloër–Holt	19, 28, 31, 46, 47	3, 21, 24, 42	—	30
5	Bruntinger Bos	19, 20, 28, 31, 38, 46	3, 16, 21, 24, 42	4	—
6	Mantinger Bos	19, 20, 28, 31, 38, 46	3, 21, 24, 42	4, 14	—
7	Eursinge	19	16, 42	6, 12, 14	34
8	Stuifzand	19, 38	3, 16, 21, 24, 42	4, 14, 33	—
9	Kynholt	19, 31	3, 21, 42	—	—
10	Asser-Bos	19, 28, 31, 46	3, 21, 42	14	—
11	Norger-Holt	20, 31, 46	3, 42	9	—
12	Ter Apel	19, 28, 31	3, 21, 42	14	—
13	Tonckens Bos	20, 31, 46	3, 21, 42	14	—
14	Aalden	28	3, 16, 24, 42	12, 14	34
15	Weerdinger Bos	28, 47	3, 10, 16, 21, 24, 42	—	34
16	Roelage Bos	19, 20, 28	3, 10, 16, 42	4	—
17	Angelsloo	28	3, 42	—	—
18	Frederiksoord	19, 31	10, 16, 21, 42	4	—
19	Wijster	19	10, 16, 21, 24, 42	4, 6, 12, 14, 33	26, 37
20	De Klencke, N.	28	3, 10, 16, 24, 42		44
21	De Klencke, S.	19, 31, 46	3, 10, 16, 21, 24, 42	—	—
22	Spaarbank-Bos	19, 31, 46	10, 16, 21, 42	4, 6, 12	43
23	Huize Echten	19, 28, 31, 46, 47	3, 10, 16, 21, 24, 42	4, 6, 14	34
24	Hollandse Veld, I	19	10, 16, 21, 42	4, 6, 12, 14	11
25	Hollandse Veld, II	19	21, 42	—	11
26	Oldengaerde	19, 28	16, 21	12, 14	—
27	Westerborker Bos	19, 20, 28	3, 10, 16, 21	4, 12, 14	11
28	Hollandse Veld III	—	3, 16, 21, 42	4, 6, 14	—
29	Hamveld	38, 46	10, 16, 42	6, 12	—
30	Westervelde	19, 28	3, 10, 16, 21, 24	9, 12, 14	—
31	Zweelo	20, 28	3, 16, 42	6, 12, 14	—
32	De Eeze	19, 31	3, 16, 21, 24, 42	4, 6, 33	—
33	Huis ter Heide	19, 20, 31, 46	3, 10, 16, 21, 24, 42	14	—
34	Lieveren	20, 31	3, 16, 42	4, 6, 9, 12, 14	23
35	Roden	20, 28	3, 16, 21, 24, 42	6, 9, 12, 14	30
36	Foxwolde	31	16, 21, 24	9, 12, 14	34
37	De Leek	19, 28	10, 16, 21	9	—
38	Zuidlaren	—	10, 16, 21, 42		—
39	Midlaren	28, 31	16, 21, 24	4, 14, 33	—
40	Noordlaren	—	3, 16, 24	12, 14	—
41	Anderse Diepje	28	3, 10, 16	6, 14	—
42	Looner-Diepje	—	16	12, 33	34
43	Roden-Peize	20	16	14, 33	—
44	Drijber	19, 28, 31	3	4	—
45	Lheebroek	19, 28, 31	10, 16, 21	4, 6, 12, 14	45
46	Ruinen, N.	19	10, 16	4, 6, 12, 14	—
47	Anser Plas	—	3, 10, 16	4, 6, 12, 14	15
48	Rhebruggen	19, 28, 31	3, 16	4, 6, 12, 14	7, 13
49	Doldersum	28, 31	3, 10, 16, 21	6, 12, 14, 33	11
50	Havikshorst	19, 31	3, 10, 16, 21, 24, 42	4, 6, 12, 33	34
51	Tiendeveen	19, 31, 46	10, 16, 21, 42	6, 12	—
52	Zuidwolde	19	10, 16	6, 12, 14	11, 18, 26, 29
53	Dickninge	19, 31, 46	3, 10, 16, 21, 42	4	—
54	Bos v. Eleveld	19	10, 16, 21, 42	14	—
55	Westerholt	19, 20	3, 42	6, 12, 14	25
56	Kraloo	19	3, 10, 16, 21	12, 14, 33	11
57	Spannen	—	16, 21	6, 12, 14	13
58	Dalfsen, N.	—	3, 16	6, 12	34, 39
59	Den Ham	—	10, 16, 24	6, 12	25, 33, 36
60	Ootmarsum	—	24	6, 33	37
61	Springendaal	—	3, 10, 16, 42	6, 8, 12, 33	—
62	Geesteren	—	3, 16, 42	4, 6, 12, 14	25
63	Tubbergen	—	3, 10, 16	12, 33	25
64	Vasse	28	10. 16	6, 33	37
65	Denekamp, N.	—	10, 24	12, 14	—
66	Tilligte-Denekamp	—	16, 21, 24	4, 6, 12, 33	—
67	Breklenkamp	28	3, 10, 16 21, 24	6, 12, 14, 33	37
68	Heemse	19	3, 10, 16, 24	4, 6, 14, 33	22, 34, 37, 41
69	Rheeze	—	16, 24, 42	14, 33	37, 41
70	Holthone	—	3, 10, 16, 24, 42	6, 12, 33	25, 37
71	De Grote Schere	19, 28, 46	10, 16, 24, 42	—	—
72	Oud-Avereest	—	3, 10, 16	12	26, 34
73	Beetsterzwaag, O.	19	3, 16, 21, 42	12	—
74	Beetsterzwaag-Oltert.	31, 46	16, 21, 24	12, 14	30
75	Heidhuizen	28, 31	10, 16, 21, 24	6, 12, 14	32
76	Koningsdiep	—	16	6, 12, 14, 33	—
77	De Driehoek	—	3, 16, 21	6	29
78	Oldeberkoop I	19	3, 16, 22	6	—
79	Oldeberkoop II	19, 31, 46	3, 16, 21, 24, 42	4	—
80	Oldeberkoop-Makkinga	19, 31	3, 21, 24, 42	—	34
81	Bekhofschans	19	21, 42	—	34
82	Linde-vallei	19	3, 16, 21	6	—
83	Bos a. Linde	19, 28, 38	3, 21, 24, 42	4, 6, 12, 14	—
84	Road to Hemrik	19, 28, 31	3, 42	—	—

TABLE III

Vegetation records of 28 Rubus stations in the Drenthian District

(An asterisk means that the species is present, but that its frequency has not been determined)

STATIONS: PLANT SPECIES:	Amer-Bos en omgeving	Anderen (bosrest)	Hegebos bij Exloo	Grolloër-Holt (O.-zijde)	Grolloër-Holt (W.-zijde)	Bruntinger-Bos	Mantinger-Bos	Eursinge, gem. Ruinen	Oude Diepje (Stuifzand)	Kynholt	Asser-Bos	Norger-Holt (Z.-zijde)	Norger-Holt (N.-zijde)	Tonckens Bos bij Norg	Aalden (bosrest)	Weerdinger Meerbos	Roelage Bos bij Ter Apel	Oeverse Bosje bij Angelsloo	Sterbos bij Frederiksoord	Dennenbos t. W. v. Wijster	De Kleucke (N.-zijde)	De Kleucke (Z.-zijde)	Huize Echten	Holl. Veld (Kerkkavel)	Holl. Veld (Rechtuit)	Westerbork (Gem. Bos)	Holl. Veld ten Z.	Dickinge bij de Wijk
no.:	1	2	3	4*a*	4*b*	5	6	7	8	9	10	11*a*	11*b*	13	14	15	16	17	18	19	20	21	23	24	25	27	28	53
I. Trees:																												
Pseudotsuga taxifolia Britt.										–	–	–		–			–	–	4.1	–		–	–	–				
Picea Abies Karsten	–	–	–		–	–				–	+.1			2.1								+.1	1.1					
Larix leptolepis Murray										–	–	–		1.1					*						–	–		–
Pinus silvestris L.	–	–	3.2							–				4.1					2.1	5.1	–	–	–	4.1		2.1	3.1	
Betula pubescens Ehrh.	3.2		+.1		+.1	1.1	3.1		*	1.1		1.1	1.1	2.2	*		+.1	3.1	+.1	2.1	*		*	3.2	1.2	1.1	1.1	+.1
Alnus glutinosa Gaertn.	+.1	1.1						4.2	3.1		–												*		–			–
Carpinus Betulus L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–				–	–	–	–	–		–		–	–	
Fagus silvatica L.	–	–	–	–	+.1	–	–	–	–	1.2	*		*			2.1			–		1.1	+.1	1.1	–		2.1	–	2.1
Quercus Robur L.	3.2	5.1	5.3	5.1	5.1	3.1	4.1		1.1	4.1	4.1	4.1	4.1	1.2	*	4.1	5.1	3.1	*	+.1	4.1	5.1	4.1	2.2	1.1	3.1	2.3	4.1
Q. borealis f. maxima (Marsk.) Ashe	–	–	–							–	–	–							2.1	+.2	–	–	*	–	–	1.2	–	–
Populus tremula L.	+.1	–	*	–	–	–	*	–	1.3	–	–	–	–	–	–		+.2							*			–	
Populus hybr. cult.	+.1	*	–	–	–	–	–	–	–	–	–	–	–	–	–													
Ulmus carpinifolia Gled.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+.1	–	–	–	–	–
Sorbus Aucuparia L.	2.2	1.2	1.2	1.1	+.1	1.2	2.1	1.2	1.2	1.1	2.1	1.1	2.2	1.2	*	3.2	4.2	2.2	+.1	3.2	2.2	2.2	1.2	1.2	2.2	+.1	2.2	+.1
Malus hybr. cult.		+.1																										
Acer pseudo-Platanus L.	–										–						*	1.1					*			+.1		
Ilex Aquifolium L.	1.2	+.1		+.1		1.1	4.2		*	4.3	3.3	4.2	3.3		*	4.3	*	4.2	–	+.1		+.1	+.2		+.2	+.2		+.2
Fraxinus excelsior L.	–	–	–	–	–	–	–	1.2	–	–	–	–	–	–														
II. Shrubs:																												
Juniperus communis L.								–												+.2								
Corylus Avellana L.	4.2	4.2	1.1	4.2	1.1	3.2		2.2	–	1.2	1.2	1.2			*							+.2	2.2					+.2
Salix cinerea L.	1.2							1.2	1.3																			
Salix Caprea L.	+.2																			–		–			–	–		
Salix aurita L.	1.2					1.2	–		1.3					1.2														
Salix hybr. div.	1.2	*					–															–						
Ribes nigrum L.	+.2						+.1	1.2	1.2										–			–						–
Rubus idaeus L.	1.3	1.3	1.2	1.2	2.3	1.2	*	2.3	*	*	1.2	*	*	1.2	*			*		1.2	4.3	3.3	1.2	1.3	1.2	3.3	1.3	1.2
Rubus Nessensis W. Hall	2.4		1.3		*	2.2	*		*	1.3	1.3	1.2	1.3	1.2	*	1.3	1.2	1.2			2.2	1.2	2.2	–		+.2	+.2	1.2
Rubus fissus Lindl.	+.3	–	–	–	–	+.2	–	–	1.2	–	–	–	–				*		*			–	+.2	+.2		+.2	+.2	
Rubus plicatus Wh. et N.	*	–	*	–	–	–	–	3.3	–	–	–	–	–	–	–				–	–			*	*			+.2	
Rubus ammobius Focke	–	–	–	–	–	–	–	1.2		–	–				*						–	–		*		+.1		
Rubus nitidus Wh. et N.	*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–				–	–	–			–			–
Rubus integribasis P. J. Müll.	1.3	–	–	–	–	–	–	–	–	–	–	–	*	–	–	–	–							–	–			
Rubus affinis Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*	*	–	+.2	1.2	1.2	+.2	*	*		1.2	–	
Rubus emergens Boul. et Malb.?	*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–				*	*	–		–
Rubus carpinifolius Wh.	*							+.2	2.2			–		1.2	*					*			*	?	–	1.2	1.2	
Rubus gratus Focke	+.2	1.3	*			1.2	–	1.2	*	–					*	*	*		+.2	1.2	1.2	+.2	*	1.3	–	3.3	3.3	
Rubus Arrhenii J. Lange	1.3				–	2.2	2.2		–		–	–	1.2	+.2		–	*	–	–	–		–		1.2	–	+.2	–	
Rubus Sprengelii Wh.	1.3	–	+.2	2.3	1.2	1.2	*		*	+.2	*	1.3	*	2.2	–	*		–	+.2	2.3	–	+.2	*		3.3	3.3	2.3	1.2
Rubus pyramidalis Kalt.	–	–	*	–	*	–	*	–	–	–				–	*	*	–		–	*	*	+.2	*		–	–	–	
Rubus silvaticus Wh. et N.	*	1.2	2.3	–	+.1	1.2				–	*				*	1.2	1.2	2.2			*	–	1.2		–	2.2	–	
Rubus egregius Focke	1.2	–	–	*	*	1.2	–	–	–	1.2	2.3	1.2	+.2	+.2					1.3			1.2	1.3	+.2	2.3			2.3
Rubus Lindleyanus Lees	–	–	–	–	–	–	–	–	1.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–				–	–
Rubus geniculatus Kaltenb.	*	1.2	–	–	–	–	–	+.2	–	–	–	–	–	–	*	*	–	–	–		–	–			–			–
Rubus vestitus Wh. et N.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*		–		–				
Rubus mucronifer Sudre	*				–	1.2	*	–	*	–	–	–	–	–		–	–	–		–					–		–	–
Rubus derasifolius Sudre	1.2		–						–	–	–				–	–			–	–	–	–		–	–		–	–
Rubus flexuosus M. et Lfv.	2.3	–	1.2	1.2	1.2	2.2	1.2	*	*	2.3	3.4	3.4	2.3	3.4	*	*	*	2.2	*	3.3	*	2.3	*	1.3	1.2	–	3.4	*
Rubus badius Focke	1.2		+.2	2.3	–	1.2	2.2	3.3	*	1.2	*	–	–	–	–	–	*		2.2	*	–	+.2	2.3	–		+.2	–	*
Rubus horridicaulis P. J. M.	–	–	–	–	–		–	–		–	–	–	–	–		–		–			*	–		–	–	–	–	–
Rubus Bellardii Wh.	1.2	3.4	–	–	4.4	2.2	*	–	–	–	1.3	2.3	3.3	2.3		–			–	–		4.4	*		–	–	–	3.3
Rubus serpens Wh.	–	–	2.4	*	*	–	–		–	–		–	–	–	–	1.3	–	–	–	–	–	–	*	–	–	–	–	–
Rosa canina L.	+.2	–	–					+.2	+.2	–			–	–			–		–					–	–	–	–	–
Rosa eglanteria L.	–	–	–	–	–	–	–	–	–	–	–		–	–		–	+.2	–	–					–			–	–
Amelanchier laevis v. villosa J. t. P.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*	1.2	+.2	+.2	–	1.2		–	*	–	+.2		–	+.2
Crataegus monogyna Jacq.	–	1.1	–	+.1	–		–	1.2	–		–		–	–	–	*	–	–		–		–	+.2	–			–	–
Prunus Avium L.	1.2	–	+.1	+.1						–	–		*	–	–	–			–	–	+.1	*		+.1				+.2
Prunus serotina Ehrh.	–	–	+.1	–	2.3	–	–	–	–		–			–	–	*			*	1.2	+.2	–	+.2	–	–	–		–
Prunus Padus L.	1.2	–	–	–	–	–	–	2.2	2.3		*			–			–	–				–	+.2	–	–	–		+.2
Prunus spinosa L.	–	2.3	*		–		–	2.2	–	–			–	–	–	–	–	–							–	–	–	–
Euonymus europaeus L.	2.2	1.2	*		–	–		–	1.2			–	–	–	–	–	–	–		–		–	+.2		–		–	–
Rhamnus catharticus L.	+.2	*	–				–		+.2			–	–	–	–	–	–	–		–		–			–			–
Frangula Alnus Mill.	2.2	–	1.1		1.1		2.2		1.2	1.2	1.2	1.1	1.2	1.2	*	2.2	*	1.2		–	+.1	+.2	+.2	*	3.2		1.2	+.2
Hedera Helix L.	2.3	3.4	1.4	3.4	3.3	1.2	3.4	–	–	2.4	3.4	2.4	3.4	–	–	2.4	*	1.3	–	–	–	–	1.3	–	–	–	–	1.3
Vaccinium vitis-Idaea L.	–	–		–	–	–		–	–	–	–	–	–	–	–	1.3	–	–	–	–		–			–	–	–	–
Vaccinium Myrtillus L.	*	–	–	–	–	–	2.3	–	*	3.4	–	–	1.3	*	–	2.4	1.3	2.3	–	–	*	*		*		–		–
Calluna vulgaris (L.) Hull	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*	–	–	–	+.2	–		–	1.3			+.2	–
Erica Tetralix L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		–	–	–		+.2	–
Sambucus nigra L.	+.2	1.1	*	–	–	–	*	–	–	–	–	–	–	–	*	–	–	1.2	+.1	+.2	3.2	–	1.2				–	+.2
Viburnum Opulus L.	+.2	–	–	+.1	–	–	*	1.2	1.2	–	–	–	–	–	–	–	1.2	–	–	–		–	–	–	–	–		–
Linnaea borealis L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+.3	–				–		–	
Lonicera Periclymemum L.	2.2	1.1	1.1	1.1	1.2	–	2.2	+.2	1.2	1.2	1.2	1.2	1.2	1.2	*	1.2	4.4	+.2	2.3	2.2	*	3.3		*	1.2	1.3		+.2
III. Dicotyledonous herbs																												
Humulus Lupulus L.	–	–	–			–	–	+.2	1.2		–	–	–		–	–	–	–	–	–	–	–	1.2	–		–	–	
Urtica dioica L.	*	2.3	–	–	–		–	2.4	3.3	–	–	–	–	–	*	–	–	–	–	–	+.3	–	+.2		–	–	–	–
Rumex Acetosella L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+.3	–	–	–	–		+.2	–	–	–
Rumex Acetosa L.	–		–		–	–	1.2	*		–	–	–	–	–	–	–	–		–	+.1				–	–			–

TABLE III. Continued

STATIONS: / PLANT SPECIES:	Amer-Bos en omgeving	Anderen (bosrest)	Hegebos bij Exloo	Grolloër-Holt (O.-zijde)	Grolloër-Holt (W.-zijde)	Bruntinger-Bos	Mantinger-Bos	Eursinge, gem. Ruinen	Oude Diepje (Stuifzand)	Kynholt	Asser-Bos	Norger-Holt (Z.-zijde)	Norger-Holt (N.-zijde)	Tonckens Bos bij Norg	Aalden (bosrest)	Weerdinger Meerbos	Roelage Bos bij Ter Apel	Oeverse Bosje bij Angelsloo	Sterbos bij Frederiksoord	Dennenbos t. W. v. Wijster	De Kleucke (N.-zijde)	De Kleucke (Z.-zijde)	Huize Echten	Holl. Veld (Kerkkavel)	Holl. Veld (Rechtuit)	Westerbork (Gem. Bos)	Holl. Veld (ten Z.)	Dekninge bij de Wijk
no.:	1	2	3	4*a*	4*b*	5	6	7	8	9	10	11*a*	11*b*	13	14	15	16	17	18	19	20	21	23	24	25	27	28	53
Rumex Hydrolapathum Huds.	–	–	–	–	–	–	–	–	1.1	–	–	–	–	–	–	–	–			–								
Polygonum Hydropiper L.	–	–	–	–	–	–	–	–		–			–			–	–			–	*							
Melandrium diurnum Fr.	*	–	–	–	–	–	–	–	–	–	–	1.2	+.2	–	–	–	–	–	–	+.1	–	–	–	–	–	–	–	+.2
Stellaria Holostea L.	*	+.2		4.4	–		4.4		–	3.4	1.4	2.4	2.3	–	–	2.4	–	1.3	*				1.3	–				[illegible]
Stellaria nemorum L.								–	–	–	–	3.4	–	–	–		–											
Stellaria graminea L.	*								–		–	–		–	–	–												
Cerastium arvense L.	–	–	–	–	–	–	–	1.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–				
Moehringia trinervia Clairv.							+.2	–	–	+.2	–	–	–	–	–	–	*	–	–	–	*	–	*	–				
Caltha palustris L.	–	–	–	–				+.2	1.3		–																	
Anemone nemorosa L.	*	4.4	–	+.3	–	–	–	–	–	1.2	1.3	1.3	*	–	–	–	–	–	–	–	–	–	2.3	–	–	–	–	1.3
Ranunculus Ficaria L.	–	4.4	–	–	–	–	–	2.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*	–	–	–	–	–
Ranunculus acer L.					–		–	1.2			–																	
Ranunculus repens L.	–	–	–	–	–	–	–	2.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Corydalis claviculata Lam. et DC.	*	–	1.2	1.2	–	1.2	–	–	*	+.2	–	1.2	1.2	1.2	*	2.3	*	1.2	1.2	1.2	4.3	2.2	1.2	–	–	4.3	1.2	–
Viola Riviniana Rchb.		–	–	+.1	–	–	–	–	–	–	–	–	–	–	–	–	*	–	–	–	–	–	–	–	–	–	–	+.2
Filipendula Ulmaria Maxim.				–				2.2	2.2	–	–			–														
Rubus saxatilis L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.3	–	–	–	–	–	–	–				
Potentilla erecta Räuschel.	*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+.1	–	–	–	–	–	–	–				
Geum urbanum L	–	–	–	–	–	–	–	–	–	–	+.2	–	–	–	–	–	*	–	–	–	–	–	–	–	–	–	–	+.2
Epilobium angustifolium L.	*	+.1	1.2	–	–	–	–	–	–	1.3	1.2	1.2	–	1.2	*	–	1.2	1.2	+.2	2.3	2.2	+.2	+.2	1.2	3.2	1.2	1.2	+.2
Circaea lutetiana L.			–			–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*	–	–	–	–	–
Oxalis Acetosella L.	*	2.2	3.4	3.3	–	1.3	*	–	–	1.3	2.3	1.3	1.3	–	*	3.3	–	2.3	–	–	*	+.3	1.3	–	–	–	–	3.4
Geranium Robertianum L.					–	–	*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+.1	–	–	–	–	–
Chaerophyllum temulum L.	–	*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Anthriscus silvestris Hoffm.	*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aegopodium Podagraria L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+.2	–	–	–	–	–	–	–	–	–	–	–	–
Angelica silvestris L.	*																											
Peucedanum palustre Moench.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+.1	–	–	–	–	–	–	–	–	–	–	–
Primula acaulis Grufb.	*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lysimachia vulgaris L.	*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*	–	–	–	–	–	–	–
Lysimachia Nummularia L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*	–	–	–	–	–
Trientalis europaea L.	–	–	–	–	–	–	1.2	–	–	–	–	–	–	–	–	–	*	1.2	–	–	–	–	–	–	–	–	–	–
Linaria vulgaris Mill.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+.1	–	–	–	–		–					
Scrophularia nodosa L.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*	–	–	–	–	–
Veronica Chamaedrys L.	–	–	–	–	–	–	–	1.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Melampyrum pratense L.	*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.3	–	–	–	–	*	+.2	–	–	–	–	–	–
Glechoma hederacea L.				–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+.2
Stachys silvatica L.	*	–	–	–	–	–	–	–	–	–	*	–	–	–	*	–	–	–	–	–	–	–	*	–	–	–	–	+.2
Galeopsis Tetrahit L.	*	–	–	–	–	–	–	+.1	–	–	–	–	–	–	–	–	–	–	–	–	+.1	–	+.1	–	–	–	+.1	–
Ajuga reptans L.			–	–	–	–	–	1.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Galium Aparine L.	*	1.2	–	–	–	–	+.2	2.2	–	–	–	–	–	–	*	+.3	–	–	–	–	–	–	–	–	–	–	–	1.2
Galium saxatile L.	*	–	+.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+.3	1.3	*	–	–	*	–	–		–
Valeriana officinalis L.				–	–	–	–	+.2	2.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–			
Solidago Virgaurea L.			–	–	–	–	*	–	–	1.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–			
Cirsium palustre Scop.						–		1.1	1.1	–	–		–	–	–	–	–	–	–									
Hypochoeris radicata L.			–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+.1	–	–	–	–	–			
Taraxacum officinale Web.	–	–	–	–	–	–	–	2.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–			
Mycelis muralis Rchb.						–	–	–	–	–	–	–	–	–	–	–	–	–	–				*			–	–	
Hieracium laevigatum Willd.			–						*	–		–								–	–	–		–	–	–	–	–
IV. Monocotyledonous herbs:																												
Maianthemum bifolium F. W. Schmidt			1.3	3.3	–	–		–	*	3.4	1.4	1.3	2.4	–	–	2.3	1.3	1.3	*	–	*	1.3	2.3	–	–	–		*
Polygonatum multiflorum Alb.			*	+.2	–	–	1.2		*	1.2	1.2	1.2	1.2	–	*	–	+.2	1.2		–	*	+.2	+.2	–		–	+.1	–
Convallaria majalis L.	–	–	–	–	–	–	–	–	–	*	–	2.3	1.4	–	–	–	3.4	–	–	–	–	+.3	+.3	–	–	–	–	1.3
Iris Pseudacorus L.	–	–	–	–	–	–	–	–	+.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Luzula pilosa Willd.					–	–	1.2		–	1.3	*	–	–	1.3	–	+.3	–	1.3	–	–	–	–	–		–	–	–	*
Carex Pseudocyperus L.				–	–		–		+.2	–	–	–	–	–	–	–	–	–	–		–	–	–	–			–	–
Carex remota Grfb.			–	–	–				–	–	–	–	–	–	–	–	–	–	–		–		*	–				–
Festuca ovina L.				–					–	–	–	–	–	–	–	–	–	–	–	–	–			–	–	–	1.3	
Festuca rubra L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+.2	–	–	–	–	–	–	–	
Poa pratensis L.	–	–	–	–	–	–	–	–	–	–	*	–	–	–	–	–	–	+.3	–	–	*	–	–	–	–	–	–	
Molinia coerulea Mnch.	–			–	–	–	*	–	–	2.3	–	–	+.3	2.3	–	+.3	–	–	+.3	+.3	–	–	*	3.3	–	–	1.3	–
Phragmites communis Trin.	–			–	–	–	–	–	1.3	–	–	–	–	–	–	–	–	–	–	–	–			–	–		–	
Holcus lanatus L.	*		+.2	4.4	–	–	+.3	–	2.3	1.3	+.3	–	–	1.3	*	1.3	+.1	1.2	+.3	1.2	3.3	1.3	1.2	+.2	2.2	2.2		1.3
Holcus mollis L.					–	1.2	–	1.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Deschampsia caespitosa P.B.	–	–	–	–	–	–	–	–	2.3	–	–	–	–	–	–	–	+.3	–	–	–	–	–	–	–	–	–		–
Deschampsia flexuosa Trin.	–	–	*	–	–	–	+.3	–	–	–	–	–	–	2.4	*	1.3	–	1.3	–	1.3	*	*	–	–	–	2.2	–	–
Calamagrostis epigeios Roth.	–	–	–	–	–	–	–	–	1.3	–	+.3	–	–	–	–	–	1.3	–	–	–	–	–	–	4.3	–	–	–	–
Agrostis stolonifera L.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.3	–
Milium effusum L.	*	4.4	–	–	–	–	–	–	–	2.3	1.3	1.3	–	–	–	–	–	–	–	–	–	–	+.2	–	–	–	–	2.3
Anthoxanthum odoratum L.		–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*	–	–	–	–	–	–	–
Phalaris arundinacea L.		–				–	–	1.3	1.3		–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–
V. Pteridophytes:																												
Equisetum palustre L.	–	–	–	–	–	–	–		+.2	–			–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Anthyrium Filix-femina Roth	–	–		–	–	–	–		–	–	+.1	–	–	–	–	–		–	–	–	–	–	1.2	–	–	–	–	
Dryopteris Filix-mas Schott	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*	–	–	–	–	–	–	+.2	*	–	–	–	–	–
Dryopteris Linnaeana Christens.	–	–	–	–	–	–	–	–	–	–	–	–	–	*	–	–	–	–	–	+.2	–	–			–	–	–	–
Dryopteris austriaca Woyn.	*	–	+.1	–	–	–	–	–	–	–	–	–	+.1	1.2	*	+.3	–	3.3	2.2	2.2	*	1.2	1.2	2.2	+.1	1.1	1.2	–
Pteridium aquilinum Kuhn	*	–	–	2.3	–	3.3	1.2	–	–	1.2	–	2.3	2.3	–	*	–	*	–	–	–	–	–	–	–	–	–	–	+.3
Polypodium vulgare L.	–		–		–	–	–	–	–	1.2	–		–	–	–	–	–	–	–	–	–	*	–	–	–	1.3	–	–

ANALYSIS OF THE PROCESS OF ANION UPTAKE OF INTACT MAIZE PLANTS

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I. INTRODUCTION

During the last years reviews of the ever increasing number of investigations into the salt absorption of plants or parts of plants appear regularly (Lundegårdh 1947; Burström 1951; Robertson 1950, 1951), so a few general remarks may suffice. It appears from the literature reviewed that a division of the absorption process according to physiological principles such as penetration into the cytoplasm or accumulation in the vacuoles is seldom made. On the other hand the analysis has been carried through so far already that physico-chemical and biochemical processes and factors take up a great place in the theoretical considerations as to the different mechanisms involved. The relationship between the salt absorption and the anion-respiration has been studied particularly and discussed thoroughly (Lundegårdh; Robertson and collaborators). For the sake of simplicity many experiments have been performed with pieces of tissue (discs of storage tissue, root-pieces, resp. excised root systems). Remarkable and for methodical reasons explainable is the use of ions like bromide, chloride and rubidium. It is clear that some care should be taken in drawing conclusions from results obtained with these ions. This also applies to founding hypotheses as to the absorption mechanism. Since uptake and metabolism appear to be intimately connected, the extent to which ions are assimilated by metabolism can be expected to influence the way in which they are absorbed.

As was already stated by ALBERDA (1948), the uptake by intact plants has as yet been studied very little. The experiments described here are a direct continuation of Alberda's. Intact maize plants were used. Mainly the uptake of phosphate was traced but occasionally the nitrogen absorption was traced. Unfortunately chloride was hardly taken up at all.

At the starting point were two problems. First the course of the uptake of phosphate and growth with low salt and high salt plants was to be determined. To be able to explain the course of uptake was the idea governing the planning of a series of experiments concerning the significance of sugar supply and growth for the absorption. Secondly, the relation between phosphate uptake and outer concentration of phosphate was studied. The problem as to what may be the nature of the first phase of the absorption and what is the cause of the well-known "saturation-phenomenon" will appear, taking an important place.

In describing the experiments, they are arranged according to a line of thought indicated below. At the end of every set of experiments a preliminary discussion will be given. By doing so, the general discussion can be restricted to the discussion of main principles and the forming of a preliminary picture of the salt absorption by intact plants.

An important question is, how far the root is permeable to the anions. The data concerning the loss of anions by the root is of interest in this respect. Intimately connected with this problem is the question of the relation of uptake and metabolism. The extent to which the metabolism plays a part, also in the very first phase of the absorption process, may be deduced from the experiments over the influence of phloridzin, sugar supply and ion-concentration of the medium.

It will appear that other processes must be assumed to have an effect on the uptake, in order to be able to explain the effect of the addition of glucose and of the "saturation-phenomenon". The correctness of this assumption will appear from the experiments about the relation between growth and uptake.

Finally an attempt must be made to explain the behaviour of the uptake in light and darkness with the aid of the data obtained in the meantime.

The experiments were performed between 1948 and 1951 at the Botanical Laboratory, Groningen. I am greatly indebted to Prof. Dr W. H. ARISZ for his constant interest and stimulating criticism. I also owe many thanks to Prof. Dr J. J. HERMANS for the instructive discussions on the theoretical aspects of the relation between concentration and uptake. Finally, I wish to thank Miss D. L. TOLMIE B. Sc. [London] for her correction of the English text.

II. MATERIAL AND METHODS

In all the experiments maize plants were used. Grains were soaked for two days and then allowed to germinate. When the coleoptiles were 3—5 cm long, the seedlings were mounted on wooden discs (11 cm diameter). In these discs were four holes. Two or three seedlings were fixed into every hole, making sets of 8—12 plants. They were grown for about four weeks on a half-strength Hoagland solution. The solution was always made with tap water. Especially at the start and at the end of the season some chlorose frequently occurred. To avoid this as far as possible, the sets were put on a minus-phosphorus solution with iron during the first week; then on a complete nutrient solution without iron. (OLSEN 1938 a, b). Better results were obtained by extending the minus-phosphorus, plus-iron period (1950). During 1951 an attempt was made to avoid chlorose by lowering the p_H of the solutions by adding diluted sulphuric acid. This provided the best results (FRANCO and LOOMIS 1947). A full-strength complete Hoagland solution could now be used without any trouble.

High salt material was obtained by renewing the solution twice a week. Especially in experiments in the middle of the summer (when the plants show a vigorous and rapid development) it appeared that the plants did not attain an extreme high salt condition. Therefore, in some experiments (1950, 1951) the solutions were changed daily just before the experiment, the plants being already in the room at constant temperature.

With low salt plants the solutions were no longer renewed after the first week. The experiments of 1948 showed that there was only a quantitative difference between the high salt and low salt plants as to the course of the uptake (exp. 6a; fig. 10). Therefore, the low salt treatment was intensified by putting the plants only once on a minus-phosphorus nutrient solution with iron. It was necessary to replenish the solutions frequently with tap water. A drawback of this last method was the inhibition of the development of the low salt material, particularly of the shoots. The rate of uptake by this material was less than that of the high salt. Because of this during 1950 and 1951 this extreme treatment was given up. It was attempted to make the high salt material as saturated as possible.

As a rule the sets were used four weeks after their having been mounted on the discs. The condition of the material at that moment was determined by the treatment and the circumstances as indicated above. Therefore, if necessary, with the description of the experiments details of these two factors will be entered into. However, to avoid any misunderstanding, we will speak of high salt plants, if the nutrient solutions were renewed frequently, and of low salt plants if this was not the case any longer after the first week. In some experiments nutrient solutions were used of a rather different composition or concentration. During the pretreatment as well as during the experiments, this sometimes happened. The p_H of these various solutions was always adjusted to 6·4—6·5. The nutrient solution used was as a matter of fact poorly buffered between p_H 3·2—6·1. Above these values there was a reasonable buffering capacity. In spite of this the p_H always rose as a result of the absorption. After absorption periods of long duration values of 7·0—7·4 were attained. Neither iron nor A—Z solution was present in the solutions, used during the experiments.

The experiments were performed in a dark room at constant temperature (21° C.). Figure 1 shows some details of the arrangement and apparatus used. In the experiments with absorption periods of 12—24 hours the sets of plants were placed on enamelled jars of rather more than one litre capacity; eight jars being fastened in a shelf (130 × 80 cm) and placed in a watertank. Moreover, on the shelf a case was constructed with a glass top and aluminium sides, allowing a good illumination. There were two compartments, which

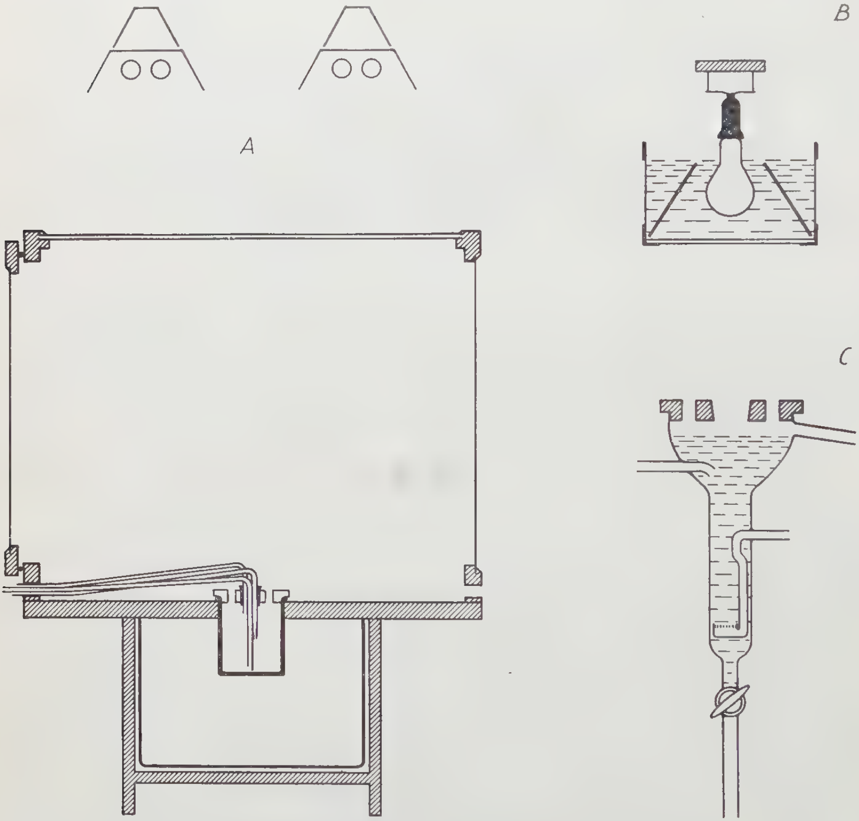


Fig. 1. The arrangement and apparatus used in the experiments. A: The complete arrangement with illumination by fluorescent lamps. Normal or carbon dioxide free air can be led through the case. B: The illumination by incandescent lamps, placed in running tap water. C: Root-chamber used in experiments with short absorption periods.

could be hermetically sealed. In this way it was possible to lead through either normal or carbon dioxide-free air (fig. 1: A).

Originally the plants were illuminated by four fluorescent lamps at a distance of 70 cm above the jars. The intensity of these lamps was rather low (5.000 lux at most). Therefore, they were replaced at an early stage by incandescent lamps. Above each set of plants one lamp of 200 Watt was mounted. In order to carry away the heat produced by the lamps by means of running tap water, they were placed four and four in two small tanks with glass bottoms (fig. 1: B). There was at both sides of the lamps a strip of mirror glass. With this light source a maximum light intensity was attained of 16.000 lux; at a distance of 70 cm 2.000 lux, the plants being illuminated by an average light intensity of 9.000 lux.

The sets of plants were always placed on one litre of a nutrient solution that was moderately aerated. The solutions were drained off by careful siphoning every 12 or 24 hours. In experiments with absorption periods of 1—4 hours a root-chamber was used as is illustrated by fig. 1: C. It was a part of an arrangement as used by Woodford and Gregory (1948) and Van Andel, Arisz and Helder (1950). It allowed a rapid changing of the solutions. Moreover, the roots could even be rinsed by distilled water within a few minutes. This is important to those experiments in which solutions of various composition were used.

The rate of uptake was determined by analysing the medium at the beginning and at the end of the absorption period. In most experiments phosphate uptake was determined, in some experiments nitrate was, and occasionally both substances were. Colorimetric methods were applied: phosphate according to the molybdenum-blue method (Parker and Fudge 1927), nitrate with the phenol disulphonic acid method (Snell and Snell 1936).

In a few experiments the nitrate content of the solution had to be determined in the presence of organic matter. The colorimetric method was less suited to this. In this case samples of 10 cm^3 of the solution were carefully evaporated to dryness. The total nitrogen content of the residue was determined according to the micro-Kjeldahl method (Loomis and Shull 1937). The results remained rather variable. By applying both methods to the same solution without organic substances, the Kjeldahl method proved to give higher absorption values than that of the phenol disulphonic acid method.

Plant material of the experiment of 1949 was also analysed. The root systems were excised, rapidly dried with filter paper and weighed. The shoots were weighed immediately and then cut into pieces. Both shoots and roots were killed by heating for 20 minutes at 110° C., and then dried for 24 hours at 65°—70° C. At the end of this drying period the dry weights were determined and the material was ground in a waring blender and stored until the next winter months. The phosphorus content was estimated colorimetrically on samples of ± 100 mg dry weight. The dry material, especially that of the shoots, being rather heterogeneous, all determinations had to be done in triplicate. In spite of this the determinations had to be repeated three times before reliable values were obtained.

The development of the shoots was chosen as a measure of the growth of the whole plants (Alberda 1948). For this purpose the distance between the wooden disc and the top of the youngest visible leaf was measured every 12 or 24 hours at the renewal of the solutions. The average increase of this distance for the 8—12 plants of each set was then taken as a measure of the growth of the plants. When a new leaf appeared, the increase in length of this one was determined henceforth. Table I shows the measurements of the individual plants of the high salt set, used in experiment 6*e* (fig. 13). As could be expected, the course of the growth of a single plant, estimated in this way, was rather irregular. Especially, when we passed on to a new leaf, a sudden fall occurred. If with a number of plants of one set a new leaf happened to appear, this irregularity occurred also in the average value. With the set of table I this was not the case; the course of the average increase in length being therefore very regular. Moreover, the regularity in the results of the experiments was increased by calculating the average growth rate of a number of sets. Of course, the regularity was greatly reduced when the number of plants was smaller (8 instead of 12) and the lapse of time between two determinations longer (24 h. instead of 12 h.). For, the probability that many of the plants produced a new leaf at the same time was increased by the longer time period, the disturbing effect not being mitigated by the greater number of the plants. This was the case in the experiments concerning the relation of growth and uptake. Therefore, in these experiments the number of young leaves which had just appeared was also given. Both data gave an impression of the development of the shoots, a rather crude index of the growth of

TABLE I

The course of the growth of the shoots of nine high salt plants. The increase in length (cm/12 hours) of the youngest visible leaves was determined. The appearance of a new leaf is indicated by *. Compare exp. 6*e* and fig. 13.

Plant number	1 day		2 days		3 days		4 days		5 days		6 days	
1	3.8	2.9	3.6	3.1	3.7	3.8	3.5	2.9	3.2	2.0	2.4	2.4
2	3.1	2.6	2.8	2.8	3.4	2.7	3.4	3.4	3.5	3.0	3.4	2.2
3	3.5	3.4	3.4	2.7	3.5	3.3	4.0	3.7	4.3	2.6	3.8*	3.1
4	2.3	6.9	2.3	2.2	2.5	2.0	2.4	2.5*	2.2	1.3	1.4	0.9
5	1.2	1.5	1.8	1.4	1.1	0.8	1.4	0.8	1.3	0.6	1.3	0.9
6	3.8	4.2*	3.5	2.7	3.9	4.0	4.7	4.4	5.2	4.1	5.2	3.8
7	3.5	3.2	4.0	3.4	3.9	3.1	4.0*	3.1	3.6	2.9	3.6	3.3
8	3.1	2.5	3.4	3.1	3.5	2.8	3.4	2.5	3.5	1.4	2.6	2.6
9	2.9	3.0	2.5	2.3	3.1*	2.0	3.4	2.8	3.2	2.7	3.2	2.8
Average growth rate	3.0	2.8	3.0	2.6	3.2	2.7	3.4	2.9	3.3	2.3	3.0	2.4

the plants, indeed. With these experiments an essential objection to this way of measuring growth came to the fore. The growth measured depends mainly on cell elongation. On the other hand, uptake proved to be connected with synthetic processes. Therefore it is more closely concerned in cytoplasmic growth. It is true that the extension growth depends on meristematic activity but the quantitative relation is rather weak. Hence, the extension growth may continue for some time, the fundamental synthetic processes being nearly stopped. It will be clear, that more exact methods of measuring extension growth (McINTYRE and WILLIAMS 1949), though perhaps giving more regular results, would have failed to overcome this fundamental difficulty. If it would have been possible to measure the rate of protoplasmic growth (e.g. as an increase in dry weight or protein content), no doubt, more striking results would have been obtained regarding the course of the growth and the relation between uptake and growth.

III. EXPERIMENTS

1. THE LOSS OF SALTS BY THE ROOTS INTO THE MEDIUM

Anions are generally assumed to permeate very slowly into the protoplasm, an active absorption being necessary by which anions are transferred from the medium through the membrane into the cytoplasm. The phenomenon of leakage of salts, so often observed in older plants, points however to an easy permeation in the opposite direction. Such a loss also occurred in one of the experiments over the relation of uptake and external concentration. This experiment, together with some experiments in which an attempt was made to obtain the phenomenon once more, will now be described and discussed.

Experiment 1a. A set of low salt plants was used to trace the effect of the external concentration on the uptake. The results of this will be described in section 4. It is important that the maximum absorption amounted to 2·4 mg P_2O_5/2h. On the second day the absorption was rather higher; the maximum rate of uptake was 3·0 mg P_2O_5/2h. It was then attempted to bring the plants rapidly into a high salt condition. For this they were placed for 2½ days on a double-strength Hoagland solution. At the same time the solution was vigorously aerated and the plants were put under a weak illumination in order to reduce the sugar content of the plants as much as possible. Then the effect of the external concentration on the rate of uptake was examined once more. The effect was studied successively of a 25, 50, 75, 100, 150 and 200 % Hoagland solution. The solution of the lowest concentration was taken first. After an absorption period of two hours it was replaced by a solution of a slightly higher concentration etc. The rates of uptake were:

—11·4 —7·0 —0·2 2·2 2·8 2·8 mg P_2O_5/2h.

So a high loss of phosphate at the start of the experiment was apparent. Doubtless this was favoured by the low concentrations. It is striking that, at the end of the experiment the same rate of uptake was attained as was obtained a few days before. The results of the nitrate absorption were:

—10·0 —7·2 —6·0 —7·6 —12·0 —18·0 mg. N_2O_5/2h.

Also in this case a high loss, decreasing during the first periods, but increasing again with the higher concentrations, was obtained. This last result is not so easily understood. At any rate this result shows that there may be a loss of nitrate and a normal uptake of phosphate at the same time. The next day the absorption of phosphate was quite normal again. With rising concentration, the rates of uptake were:

1·0 2·1 2·5 3·0 2·9 2·8 mg P_2O_5/2h.

The uptake at the highest concentrations again showed the same maximum rate as it did at the start of the experiment.

Experiment 1b. Just as for the first experiment a low salt set (cultivated August—September 1950) was used. It was put immediately on a Hoagland solution of double-strength to bring it into a high salt condition. Moreover, the light intensity was reduced after two days. On the fourth day the set was placed on a half-strength Hoagland solution. The solution was renewed every two hours. The course of the uptake was:

—0·78 0·00 0·64 0·77 0·93 1·14 mg P_2O_5/2h.

Then the plants were placed in darkness for two days. A minus-nitrogen nutrient solution (200 %) was used. After this treatment the uptake on a 50 % Hoagland solution amounted to 0·32 and 0·21 mg P_2O_5/2h. There was no loss of phosphate. The treatment was continued immediately for another two days. The rate of uptake was then: 0·00 and 0·40 mg P_2O_5/2hours.

After this the set was placed on a double-strength complete Hoagland solution again. The next day the uptake was determined again on a half-strength solution:

—1·57 —0·49 0·03 0·07 mg P_2O_5/2hours.

So there was a loss of phosphate after a dark treatment, the plants being placed on a nutrient solution of high concentration. A high nitrate concentration proved to favour particularly the loss of phosphate.

Experiment 1c. For this experiment a set of low salt plants was used again (grown August—September 1950). As a result of the unfavourable circumstances the vegetative growth was greatly checked, so that the plants though being 7—8 weeks old, were but little more developed than were the previous sets. On the other hand these plants showed an incipient flowering. In order to bring the plants into a high salt condition they were placed for two days on a full-strength Hoagland solution. The plants remained in the light throughout the experiment. The uptake was studied on the same day on two different concentrations. On a full-strength Hoagland solution the course of uptake during three successive absorption periods was:

—0·46 0·26 0·42 mg P_2O_5/2h.

Immediately after this on a weaker solution viz. 25 % Hoagland solution:

—0·36 0·04 0·12 mg P_2O_5/2h.

On lowering the concentration a loss was obtained which soon changed into a normal active uptake again.

Then the pretreatment was continued; after this the uptake resp. loss of phosphate was again estimated on three different concentrations during nine successive absorption periods. The results were:

On the 200 % Hoagland solution:

—0·40 —0·20 —0·18 mg P_2O_5/2h.

Then on the 100 % Hoagland solution:

—0·22 0·10 0·08 mg P_2O_5/2h.

Finally on the 25 % Hoagland solution:

—0·09 0·07 0·07 mg P_2O_5/2h.

The increase of the uptake was less pronounced in this case as a result of the highly diminished absorption activity. Because of this the differences at the transition to a solution of lower concentration were less striking.

Experiment 1d. In this experiment a high salt set was used, grown under artificial illumination (November 1950). The plants were three weeks old and displayed a vigorous vegetative growth. Because of this they were not in an extremely high salt condition. Therefore the set was put on a complete Hoagland solution for four days and then in darkness on a solution of double-strength for two days. No loss was obtained either on a double-strength Hoagland solution or on a full-strength solution or a half-strength one. The pretreatment was continued for a week on a double-strength Hoagland solution in darkness. After this the course of the uptake on a full-strength solution was:

? —1·44 —0·88 —0·48 0·00 0·16 mg P_2O_5/2h.

It can be concluded that only by a dark treatment of long duration could a loss be obtained with young, vigorously developing material.

Discussion

It has been known for a long time that roots may show a loss of substances. Originally interest was directed towards the acids and organic compounds (dissolving capacity; interaction problems). Later on, inorganic substances were also found to be excreted. It remained uncertain for a long time if this loss was based on an injurious effect, a dying off of the rootcells, or on a normal physiological function. That the latter probability may apply was proved by an extensive investigation of ACHROMEIKO (1936).

Many investigators have pointed out the importance of the phase of development to the rate of uptake and loss. This conclusion has been mainly based on analysis of material at various moments during the development. Mostly it is only the aerial parts that have been harvested and analysed. The amount of inorganic substances was often found to diminish during the flowering stage. There must have been a loss of salts from the shoots to the roots. Though a proof has not been given of the hypothesis that ions are lost by the roots, this is very probable. The salt content of the roots is tending to decrease rather than to increase during this stage (ACHROMEIKO).

It is obvious that the occurrence of leakage depends on the external conditions e.g. the availability of nutrients. Besides this however, the type of the plant is important. Loss of substances is generally found with plant species showing a marked difference between the vegetative stage and the flowering one (MAXIMOV 1938). Potassium is always lost very easily but a loss of phosphate is often obtained too (HORNBERGER 1882; BURD 1919; WILFARTH, RÖMER und WIMMER 1906; ACHROMEIKO 1936; DELEANO und ANDREËSCO 1932; ASANA 1949; KNOWLES and WATKIN 1931; VAN DER PAAUW 1948; WILLIAMS 1948).

In physiological experiments a loss by the roots was also met with. Thus, HUMPHRIES (1950, '51) found with excised root-systems a loss of phosphorus, nitrogen and potassium. Particularly potassium is readily given off e.g. as a result of a dark treatment (LUTTKUS und BÖTTICHER 1939; VAN ANDEL, ARISZ and HELDER 1950).

In accordance with this evidence from the literature it was found that with plants already in the flowering stage, a loss of phosphate appeared easily. Younger vigorously developing material being used, a check of the development e.g. by a dark treatment was necessary. A second condition was a pretreatment with a nutrient solution of high concentration. The effect of the nitrate concentration was remarkable. The meaning of this is not yet quite clear. Achromeiko pointed out the fact that an excretion by the roots during the flowering stage mainly occurred with plants rich in proteins. He assumed a relationship between protein metabolism and loss of minerals. This enhanced the impression of the plants having to be in a condition comparable with that of plants in the flowering stage. Then dissimilation is dominant, resulting in an increase of the concentration of non-metabolized substances. As soon as the external concentration is lowered a certain amount of salt will be given off until a new equilibrium has been established.

Where the phosphate lost came from was not traced. From the literature mentioned above it can be concluded that with plants in the flowering stage the shoot particularly looses the substances. This concerns however a loss during a prolonged period. LUTTKUS und BÖTTICHER showed that the potassium excreted by the roots in darkness, was mainly derived from the shoot. However, potassium is generally assumed to be easily transported. Anions will be transferred much more slowly. Hence, the phosphate given off in these short experiments, may be supposed to come nearly exclusively from the roots. By this it is not yet decided whether the ions come from the symplasm or from the vacuoles.

The exosmosis of substances by cells or tissues may be the result of an injurious effect e.g. by a sudden change of temperature of the medium; by using unbalanced solutions, narcotics or toxic substances. By this the semipermeability of the cytoplasm is lost most often, so that substances of the vacuoles may permeate outwards e.g. the anthocyanin of the beetroot. It is not very likely that the loss by the roots of the experiment mentioned here, would be the result of damage, for the rate of loss of phosphate decreased rapidly, and changed into an uptake that could be as high as the uptake was before the plants had been brought into a condition favourable to loss. Moreover a loss of nitrate was found to occur, the phosphate being absorbed actively at the same time. Hence it may be concluded that the loss of salts from the symplasm is mainly or perhaps exclusively concerned. This might mean that the symplasm is highly permeable to salts. ARISZ (1945) and WIERSUM (1947) arrived at the same conclusion. For a complete exposition of the subject and a discussion of the literature these authors may be referred to. With the exception of the data about the loss of ions they point to the experiments of RUFZ DE LAVISON (1910); the promoting effect of the transpiration stream on the absorption (FREELAND 1937; SCHMIDT 1936); the exchange phenomena as they have been especially studied with radioactive substances (OVERSTREET and BROYER 1940; BROOKS and BROOKS 1941) The resistance so often found in experiments on permeability must be situated mainly in the tonoplast. Meanwhile, ROBERTSON (1950, 1951) also cautioned against an overestimation of the importance of an outer membrane of the cytoplasm. He points to the possibility that a slow diffusion rate of anions may also depend on the presence of large indiffusible organic anions in the cytoplasm. He puts greater value on explanations based on the Donnan-theory. The picture of the process of loss of ions just mentioned, is in accordance with this. The plants being in a normal active condition, the free anion content of the cytoplasm will be low (ARISZ 1945). Only at special conditions, when metabolic activity is low, can the concentration increase and an obvious loss may occur, the external concentration being considerably lowered. Especially the fact that the leakage was dependent on the external concentration made it seem likely to be a passive process.

Attention should be drawn to one difficulty in this concept. One condition for the occurrence of a Donnan equilibrium between tissue and medium is that the cytoplasm may be considered a gigantic, immobile and polyvalent colloid ion (FREY WYSSLING 1948). In such a cytoplasm, transfer of anions can be expected to be highly impeded, and BRIGGS and ROBERTSON (1948) found diffusion of anions in tissue discs to be very slow indeed. The rate of loss found in these experiments, seems to be in conflict with these findings. However, it is uncertain whether the salts were lost as molecules or as ions. Moreover, it is unknown where the salts came from, so that it is impossible to decide if there has been a transport over a long distance. Compared with the absolute amount of phosphate in the roots (at a rough estimation 20—30 mg P_2O_5) the amounts given off were not high. But to this amount the phosphate, not available or not easily available for loss also belongs. It is impossible therefore, to get an impression of the quantitative meaning of the loss found. No more do the experiments of WIERSUM (1947) give clear results, the data concerning the precise anion permeability of the root tissue being far from complete. In the opinion of the author, they point to a low passive permeability; the phosphate and nitrate transfer obtained can be considered as a normal active secretion into the xylem vessels. On the other hand experiments over the exchange with isotopes point to a rather rapid transfer possibility. Therefore principles other than passive diffusion may play a part e.g. surface migration (BROOKS and BROOKS 1941; JENNY and OVERSTREET 1939). To what extent such phenomena of accelerated diffusion are important, is difficult to say. It may be that it has a meaning for the transport in the walls of the cells of the cortex (ROUSCHAL und STRUGGER 1940), by which the whole of the cortex cells is in direct contact, so to speak, with the medium (PREVOT and STEWARD 1936; WIERSUM 1947). The surface of the cytoplasm now being permeable to anions, the ion content of the symplasm can be brought rapidly into equilibrium with the external concentration.

The leakage is generally assumed to be a passive process. In agreement with this assumption it has been attempted up to now to explain the processes with the aid of physico-chemical principles such as diffusion or accelerated diffusion. This does not exclude other transport principles more closely related to metabolism. Thus, protoplasmic streaming will be of direct importance to the loss of ions, because of its levelling concentration gradients arisen from that loss. The connection between absorption and metabolism will come up for discussion in the next sections. To what extent the leakage has to be considered in an analogous way will be discussed in details in the general discussion.

2. THE INFLUENCE OF PHLORIDZIN ON THE UPTAKE

The view that metabolism, particularly of respiration, is of importance to the salt absorption is nowadays generally accepted. The most important facts that have led to this view are: the capacity to accumulate ions against a large concentration gradient; the necessity of a good oxygen supply; the high dependence on temperature. In these experiments also the effect of the air supply on uptake was clearly demonstrated in those cases where some stagnation of the aeration occurred. Even in experiments with absorption periods of only two hours, the uptake of phosphate decreased immediately and could sometimes even stop.

In particular, the investigations with inhibitors (LUNDEGÅRDH, MACHLIS, ROBERTSON, ARISZ) have demonstrated the connection between ion absorption and metabolism very clearly. On the grounds of such investigations LUNDEGARDH holds the cytochrome-oxydase system responsible for the absorption mechanism. Robertson and collaborators have been able to corroborate this view with discs of storage tissue and pieces of roots, as also has ARISZ with *Drosera* tentacles and leaf strips of *Vallisneria.*

It was quite natural that it was asked, to what extent the phosphorylation processes, being so closely coupled to the dissimilatory processes, have significance for the uptake too (HOAGLAND 1948; NANCE 1949). ROBERTSON, WILKINS and WEEKS (1951) therefore traced the effect of 2,4-dinitrophenol on the active salt absorption. As a matter of fact, they obtained an obvious inhibition. However, they point out the fact that the inhibition may be due to some injurious effect on protoplasmic structures essential to the absorption mechanism.

It is clear that phosphorylation processes may have a binary significance on the uptake of phosphate, phosphorus being used up in these processes too. That is why the influence of inhibition of these processes on the uptake of phosphate was studied. As an inhibitor, phloridzin was used, as it is generally considered to be a harmless substance. Only weak concentrations were used. The experiments were performed in the same way as was described in the previous section. A complete, full-strength Hoagland solution (p_H: 6·4—6·5) served as a nutrient solution. Phloridzin was added up to concentrations of 10^{-4}—10^{-3} molarity. The substance is poorly soluble at room temperature. By heating up to 60° C. this trouble can easily be overcome. It is of primary importance to trace the influence on the uptake of other anions along with the influence on the phosphate absorption. Therefore, in some experiments both the uptake of phosphate and of nitrate were determined. The presence of phloridzin gave some trouble because of its disturbing effect on the phenoldisulphonic acid method. Therefore, a nitrogen determination by the micro-Kjeldahl method was occasionally made. The precision of the determinations of the nitrate uptake was not very high.

This examination had to be cut short. For that reason, results and conclusions are highly preliminary. However, they are in full agreement with the results obtained by ARISZ (1952) with *Drosera* and *Vallisneria.*

Experiment 2a. In this experiment two sets were used, each consisting of twelve, three week old plants. To be sure of a sufficient rate of uptake, absorption periods of three hours were taken. During the first day the plants were intensively illuminated. There were four absorption periods. During the second and the fourth period, phloridzin was added to the solution.

The first set was placed first on a concentration of 10^{-3} mol. phloridzin and then on a concentration of $3 \cdot 2 . 10^{-4}$ mol. The rates of uptake were:

Phloridzin concentration:	0	10^{-3}	0	$3 \cdot 2 . 10^{-4}$	mol.
Uptake:					
	1·73	*1·42*	1·10	*1·08*	mg P_2O_5/3h.
	18·2	?	20·1	?	mg N_2O_5/3h.

There was an obvious inhibition of the uptake of phosphate at the higher phloridzin concentration. The inhibition was continued during the third absorption period when phloridzin was no longer applied. Hence there was an after-effect. The low concentration did not show any influence.

The nitrate determinations of this experiment were made colorimetrically. Phloridzin proved to interfere. Hence, the nitrate uptake could not be determined during the second and fourth absorption period. There was no inhibition of the nitrate uptake during the third period, as was the case with the uptake of phosphate.

The second set was placed first on a low concentration of phloridzin (10^{-4} mol.) then on a rather higher one ($3 \cdot 2 . 10^{-4}$ mol.). The course of uptake was:

Phloridzin concentration:	0	10^{-4}	0	$3 \cdot 2 . 10^{-4}$	mol.
Uptake:					
	1·32	*1·32*	1·36	*1·31*	mg P_2O_5/3h.
	18·2	*19·2*	22·3	?	mg N_2O_5/3h.

There was no question of any inhibition either of the phosphate uptake or of the nitrate uptake.

Summarizing, it can be stated that phloridzin could have an inhibiting influence on the phosphate absorption. Whether the nitrate absorption can be inhibited too, could not be settled. In any case the nitrate absorption turned out to be less sensitive to the addition of phloridzin.

Both sets were subsequently placed in darkness. The next day the inhibiting effect of phloridzin was investigated again. At the same time the influence of glucose addition (2 gm per 300 cm³ solution) was examined. The first set was successively put on a Hoagland solution, a solution with phloridzin ($3 \cdot 2.10^{-4}$ mol.), a solution with both phloridzin and glucose, and a solution only with glucose. The rates of uptake were:

1·17 0·77 0·88 1·13 mg P_2O_5/3h.

As a result of the dark treatment the level of the uptake activity was lower than it was the day before. Moreover, there was an inhibition of the uptake at a phloridzin concentration of $3 \cdot 2 \cdot 10^{-4}$ mol. By adding glucose the uptake was but little increased. The phloridzin being removed, the uptake rose immediately however and there was no after-effect.

The second set was treated in the same way only the phloridzin concentration was slightly higher viz. $5 \cdot 6 \cdot 10^{-4}$ mol. The course of the uptake was:

$$1 \cdot 04 \qquad 0 \cdot 42 \qquad 0 \cdot 73 \qquad 0 \cdot 99 \text{ mg } P_2O_5/3h.$$

The course was comparable with that of the first set. The inhibition was much stronger and so was the favourable influence of the glucose, even in the presence of phloridzin.

In all cases in which phloridzin had been added, the solutions were faintly yellow in colour after having been in contact with the roots. The colour intensity was proportional to the phloridzin concentration used. With the lower concentration (10^{-4} mol.) the colour could hardly be distinguished. If the solutions used were stored, the colour turned deeper. Contrary to this, solutions with phloridzin, not having been in contact with the roots, were only after days coloured very faintly. Also the solution without phloridzin, used after a period in which phloridzin had been added, were obviously, though more faintly coloured. This could not be a consequence of some residue of the solution used before, for the roots were rinsed thoroughly when changing the media. STREET and LOWE (1950) impute this colouring to some impurity of commercial phloridzin: in their opinion it cannot be due to hydrolysis of phloridzin. At any rate, both the velocity at which colouring appeared in these experiments and the fact that an obvious after-effect sometimes could be seen, do point in that direction. Phloridzin has a large molecule and permeates passively with difficulty, as does raffinose. But the after-effect of the inhibition and the colouring of the solution without phloridzin used afterwards, pointed to a permeation of the phloridzin.

The same sets were used in the next experiment, the plants being five weeks old. Phloridzin concentrations of 10^{-4}—10^{-3} mol. were successively added. The maximum inhibition amounted to 41 %. This was already attained at $4 \cdot 6.10^{-4}$ mol. There was an obvious after-effect. On the second day there was even some stimulation of the uptake at a low concentration. Such a stimulation also occurred after the addition of glucose. If besides, phloridzin was added to this solution with glucose no alteration of the uptake was observed.

Experiment 2b. From the previous experiment it appeared that there can be an after-effect of the phloridzin inhibition. Because of this it is impossible to trace the influence of the phloridzin concentration by putting the plants successively on solutions with varying amounts of phloridzin. Therefore on five consecutive days of this experiment the uptake was determined during five absorption periods every day, on a complete Hoagland solution, phloridzin being added during the third absorption period. In this way the effect of four different concentrations of phloridzin was studied. Two sets of twelve plants were used, a high salt set and a low salt one. They had been grown under unfavourable circumstances (August—September 1951). That is why they were put into the room of constant temperature five days before the experiment and cultivated under artificial light. They must have been in a high sugar condition. The results are summarized in table II. With 10^{-4} and $2\cdot1.10^{-4}$ mol. there was a stimulating effect on the phosphate uptake; with $4\cdot5.10^{-4}$ and 10^{-3} mol. an inhibition. Again there was an after-effect of the phloridzin treatment. It was striking that this after-effect, on the first two days consisted of an inhibition, though a stimulation was found in presence of phloridzin. On the last day, as a stimulation was obtained too, the decrease afterwards was less pronounced. Hence in spite of this decrease the rate of uptake remained a little higher than it was during the first two absorption periods. The absorption level on this day however, was somewhat lower than it was during the previous days.

TABLE II

The influence of various phloridzin concentrations on the uptake of phosphate. The phloridzine was applied during the third absorption period of each day at the concentration indicated.

Phloridzin concentration	1	2	3	4	5	
10^{-4}	1.44	1.49	*1.70*	1.28	1.26	High salt mg P_2O_5/2h
2.1×10^{-4}	1.36	1.32	*1.60*	1.19	1.17	,,
4.5×10^{-4}	1.39	1.45	*0.87*	0.91	0.81	,,
10^{-3}	1.17	1.49	*1.04*	1.10	1.14	,,
10^{-4}	1.05	0.95	*1.30*	1.12	1.08	,,
10^{-4}	0.04	0.43	*0.47*	0.36	0.43	Low salt mg P_2O_5/2h
2.1×10^{-4}	0.70	0.75	*1.02*	0.66	0.74	,,
4.5×10^{-4}	1.07	0.85	*0.44*	0.34	0.31	,,
10^{-3}	0.84	0.94	*0.51*	0.68	0.71	,,
10^{-4}	0.72	0.72	*0.95*	0.84	0.85	,,

Experiment 2c. The last experiment, in which an inhibition was obtained, was performed in October 1951. It was necessary to grow the material during the last week in the room of constant temperature under artificial light. The uptake during five periods of two hours was determined. During the third period phloridzin was added in a concentration of $5\cdot10^{-4}$ mol. The uptake of nitrate was also determined by analysing samples with the aid of the micro-Kjeldahl method. The results were:

Set I	0·80	0·80	*0·64*	0·80	0·83	mg P_2O_5/2h.
Set II	0·50	0·51	*0·33*	0·53	0·66	mg P_2O_5/2h.
Set I	92·9	92·3	*89·4*	91·6	91·8	mg N_2O_5/2h.
Set II	94·7	94·0	*90·8*	104·0	104·0	mg N_2O_5/2h.

No doubt, the nitrogen determination supplied absolute values too high for the nitrate uptake. These figures have therefore only a relative value. At any rate, both the phosphate and the nitrate uptake were inhibited. The inhibition of the phosphate uptake amounted to 20— resp. 37 %; the values for nitrate were 3— resp. ± 5 %. There was no clear after-effect.

Discussion

In an occasional supplementary experiment no inhibition was found. The material of this experiment was in bad condition (grown October 1951) and showed only a slight absorption. It was remarkable that the solutions were not coloured in these cases. Thus, there is a relation between inhibition and after-effect on the one hand and the colouring of the solutions on the other hand. This needs further examination. The importance of the condition of the material may be derived from the results concerning the influence of light and darkness and of the glucose supply on the action of phloridzin. This last might point to some competition between sugar and phloridzin, as was assumed by STREET and LOWE (1950), as to the phosphorylation processes, enabling the sugar absorption to take place. This assumption too requires further investigation.

This preliminary study has clearly shown the possibility of checking the uptake of phosphate, while at the same time perhaps the uptake of nitrate is checked to a far lesser degree. This last does not necessarily imply that phosphorylation processes are without importance to the nitrate absorption. It only makes it seem very likely that the phosphate uptake is dependent on this process to a much higher degree. This is quite understandable if the phosphate uptake is assumed to be determined by the measure in which phosphate is used up in these phosphorylation processes. This assumption is in accordance with that which is known about phloridzin action. Though there is no agreement as to the way in which phloridzin checks these phosphorylations, it is certain that the direct or indirect result is a blocking of the formation of hexose-phosphate (SHAPIRO 1947). Besides this, investigations with radioactive isotopes have shown that instable phosphate esters (gel-P: Green 1951), adenosine tri-phosphate and hexose-phosphate belong to the first and very rapidly formed products of the phosphate metabolism (HAUROWITZ 1948). It seems legitimate to conclude, that the formation of an organic phosphorus compound constitutes an essential part of the phosphate absorption process. Moreover, it must be primary in every form of phosphate uptake, since inhibition by phloridzin occurs with low salt as well as with high salt material. This view will be further dealt with particularly in the section on the relation between uptake and external concentration.

3. THE IMPORTANCE OF THE SUGAR SUPPLY FOR THE UPTAKE OF PHOSPHATE

If the uptake of phosphate is so intimately connected with metabolism (respiration, phosphorylation), the sugar condition of the plants can be expected to be of primary importance. The significance of the salt condition for the uptake is well-known (Hoagland and Broyer 1936). Many experiments, for that reason, are performed with high salt as well as low salt material. Now the roots of both types of plants differ in sugar content too. As could be expected, Alberda (1948) found roots of low salt plants to have a higher sugar store than have high salt plants. Therefore, one can wonder if the differences between the uptake, in particular between the uptake of phosphate of low salt and high salt plants should not be ascribed to the sugar condition rather than to the salt condition. In this relation Phillis and Mason's finding (1940 *a*, *b*), that with cotton plants the uptake is to a high extent dependent on the supply of substances from the shoot, is important. Ringing the plants depressed the uptake of bromide by the roots within a few hours. When the plants had been amply illuminated, the effect was much less.

Alberda investigated the influence of light and darkness on the phosphate uptake of high salt plants. In darkness the rate of uptake decreased rapidly. However, the growth of the shoots showed a similar course. Since the plants were in a high salt condition, Alberda assumed the growth of the shoot to have a determining influence on the uptake by the root. As a result of the diminished utilization, a part of the phosphate supplied by the roots, was carried back to the roots, which had a damping effect on the uptake from the external solution. So in the first place the salt condition was held responsible for the course of the uptake found.

In order to trace the importance of the sugar supply for this course of the uptake a few experiments were performed, in which the plants were brought into a carbon dioxide-free atmosphere. As will appear, results could be obtained virtually equal to those obtained by a dark treatment. Besides, further inquiries into the influence of glucose addition to the nutrient solution were made. As was found already by Van Andel, Arisz and Helder (1950), the phosphate absorption is increased by sugar supply even in the light. These experiments were only carried out with high salt plants. They were continued and extended by the author. In addition to high salt, low salt material was also examined. Moreover, an attempt was made to trace the extent to which the growth of the shoot may have an influence on the uptake, at the same time.

Experiment 3a. To trace the influence of the withdrawal of carbon dioxide on the phosphate uptake, two sets of twelve high salt plants, six weeks old, were used (grown June—July 1948). Use was made of the complete arrangement, shown in fig. 1 : A. On the first day the uptake was determined with the case opened. After this the case was closed. Carbon dioxide-free air was led through for four days. Finally normal air was used for six days. On the last day the case was opened again. Figure 2 represents the average result of the two sets. It clearly shows that the uptake immediately fell on carbon dioxide deficiency.

The course can be completely compared with the behaviour of the plants coming into the darkness (fig. 12, 13). The increase of the uptake, the plants being in normal air again, was slight but steady,

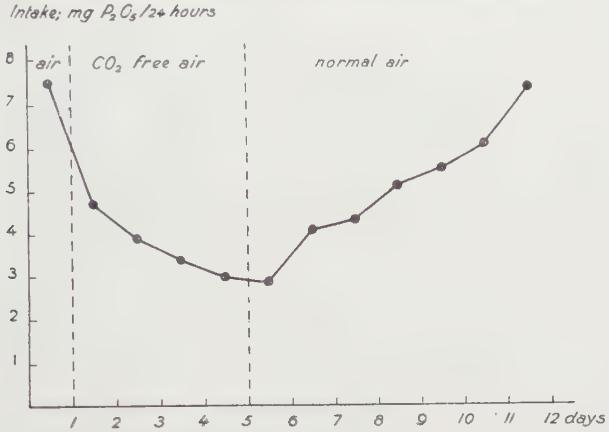


Fig. 2. The course of phosphate uptake by high salt plants in normal and carbon dioxide free air. The plants were illuminated continuously.

so that in the end the original level was nearly obtained. It is possible that the isolation of the shoots in a confined space constituted less favourable circumstances.

Experiment 3b. A corresponding experiment was also made with low salt plants. The plants were in the closed case throughout the experiment. With two sets, normal air was led through during the first two days and then carbon dioxide-free air during the last two days. A third set was placed immediately in carbon dioxide-free air and afterwards into normal air. The results are represented by table III.

TABLE III

The influence of the withdrawal of carbon dioxide on the course of the uptake of phosphate by low salt plants (exp. 3*b*)

	1 day		2 days	3 days		4 days	
		$+ CO_2$			$- CO_2$		
Set I	10.5	—	9.8	9.0	—	8.4	mg P_2O_5/24h
Set II	10.6	—	10.4	10.4	—	6.2	,,
		$- CO_2$			$+ CO_2$		
Set III	13.0	—	7.7	5.8	—	6.7	mg P_2O_5/24h

Low salt material has a higher sugar content and as a matter of fact only a slight effect from the withdrawal of carbon dioxide was obtained with set I. The other sets showed an obvious decrease as did the high salt sets. This gradual difference between low salt and high salt material has also been found in the experiments concerning the influence of light and darkness (fig. 10).

Experiment 3c. A low salt set was grown under artificial light. The plants were then in a high sugar condition. With these plants the effect of sugar supply was traced. The set was placed on the root chamber (fig. 1: C) with 400 cm³ nutrient solution. This solution was changed every two hours. In this way the uptake was determined during seven two-hours periods on one day. The set was placed in darkness throughout the experiment. This is why the sugar supply could be expected to decline gradually. The course of the uptake was determined on the first, third, fifth and seventh day. On these days glucose was added (2 gm per 400 cm³ solution) during the third, fourth and fifth absorption period (fig. 3). To prevent the plants as far as possible from getting into a high salt condition, they were put on tap water during the remaining days.

In spite of their being in darkness, the plants showed a larger uptake on the third day than they did on the first one. Such an increase of the phosphate uptake was always found with low salt material, as will appear from the next section. It depends on the lack of salts, in particular, on phosphate deficiency, by which the growth and the absorption activity is impeded. The increase occurred in the dark in this experiment. This means that the sugar supply was not yet a limiting factor. Accordingly it is understandable that addition of glucose as yet had no effect. Moreover, it is remarkable, that the uptake showed a decreasing tendency at the start of the third, fifth and seventh day. It is possible that this higher uptake during the first absorption period depended on the plants having been on tap water continuously for about 38 hours. The influence of glucose administration was becoming more pronounced during the course of the experiment. Whereas hardly any influence could be observed on the first and third days, there was a more obvious effect on the fifth day. And on the last day as the plants had been in darkness for a week, the effect was very striking.

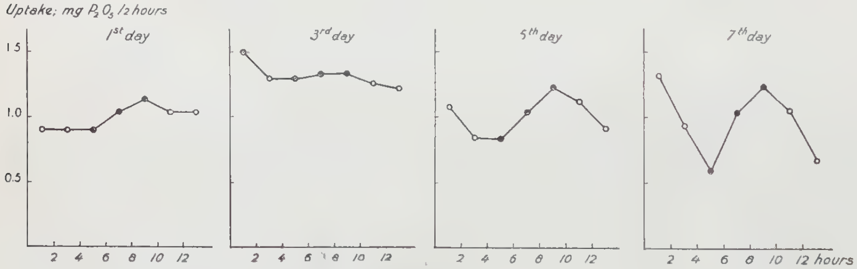


Fig. 3. The influence of glucose addition (•—•) on the phosphate uptake by low salt plants in darkness.

Experiment 3d. A high salt set was used, grown under the same circumstances as the low salt set of the previous experiment. As will appear, this set had at its disposal a sufficient amount of sugar. With respect to methods this experiment was like the previous one. On the first day it was traced to see whether the administration of various amounts of glucose brought about an enhancement of the uptake. Successively 0·5, 2 and 4 gm glucose were added to 400 cm³ nutrient solution. None of the concentrations used had any effect (fig. 4).

The next day the shoots were excised at the end of the first absorption period. If a part of the amount of phosphate supplied by the roots was transported back from the shoots, owing to the dark treatment, an enhancement of the uptake from the medium could be expected to occur as soon as the shoots were removed. In fact, the uptake continued undisturbed at the same rate during the whole day. For that reason, an important loss from the shoots did not occur under the given conditions. Some exudate appeared at the stumps, that was blotted with filterpaper. The amount of phosphate present in this, was determined. The volume of the exudate decreased rapidly during the course of the day. At the end hardly any exudate was to be seen. As figure 4 indicates, the total amount of phosphate decreased too. (The method of estimation was rather a crude one).

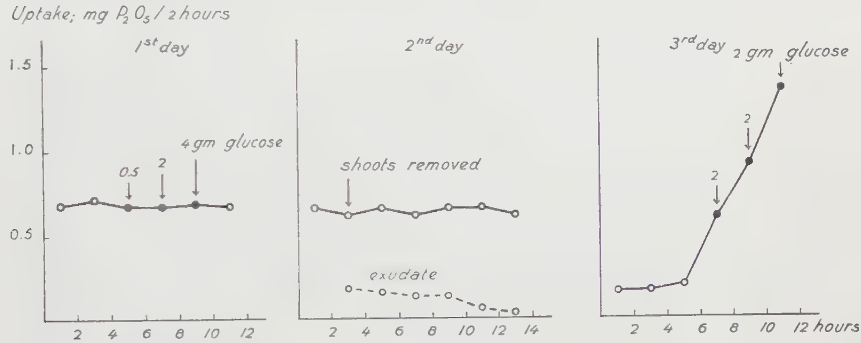


Fig. 4. The influence of glucose addition (•—•) and the removal of the shoots on the phosphate uptake by high salt plants.

On the third day the rate of uptake had become much lower. At this time the addition of 2 gm glucose enhanced the uptake immediately. It was very striking here that the enhancement continued to increase, so that finally the absorption rate of the intact plants on the first day was surpassed. The next day the uptake was low again (not represented by fig. 4). Addition of glucose had but slight effect.

Experiment 3e. The previous experiment was repeated in a somewhat different way with an older and more developed high salt set. After the uptake of the intact plant had been determined, the three uppermost, rapidly growing leaves of all eight plants were drawn loose. There remained on every plant three full-grown leaves. During the three following periods no marked influence was to be seen. At the end of the fourth period shoots were entirely excised as was done in the previous experiment. In this case the uptake fell immediately. This fall could be changed into an increase by adding glucose during the last absorption period. The exact course of uptake was:

6·0 6·0 6·2 5·6 2·2 3·4 mg P_2O_5/2h.

This result supports the assumption that the sugar supply from the shoot has a strong influence on the phosphate uptake from the medium.

Discussion

All experiments mentioned, confirmed the supposition that the sugar supply is very important for the phosphate uptake. Humphries (1950, 1951) found with excised root systems of barley plants that the uptake of nitrate and phosphate was enhanced by the administration of sugar (Broyer 1951). In particular, the phosphate uptake was sensitive.

Street and Lowe (1950) studied the inverse relationship. They found sugar absorption by root cultures of tomato plants to be favoured by increasing the external phosphate concentration. Hence they assumed the sugar absorption to be coupled with phosphorylation processes. This idea was supported by the inhibitory effect of phloridzin on the growth of the cultures. Such an absorption of sugar means at the same time an absorption of phosphate. Whether the first phase of the phosphate absorption can be explained completely by this, cannot yet be decided, though it renders the intimate connection of phosphate absorption and the sugar relations understandable. On the other hand the experiments of the previous section pointed to the significance of phosphorylation processes, so that a chemical binding of the phosphate as an essential step in the absorption process became likely.

In any case, the stimulating influence of sugar addition also on the uptake of other ions, indicates that sugar influences the absorption process in a more general way as well, e.g. by enhancing the growth. Prevot and Steward (1936) found the uptake of bromide by excised high salt roots to be enhanced to such a degree by 2 % glucose, that even the absorption level of low salt roots was attained. They hold the limited growth of excised high salt — low sugar roots responsible for the low absorption velocity. With intact plants growth of the roots is possible as a result of sugar supply from the shoots. At the same time a transport of salts into the shoots is possible.

The effect of the growth of the shoots could not be demonstrated. It will be clear that the dominating significance of the sugar supply for phosphate uptake does not mean that the growth of the root and shoot are of no importance to the uptake. On the contrary, the influence of sugar may depend entirely or partly on its effect on the growth. Further evidence is necessary however. This will be produced in the next section.

4. THE RELATION BETWEEN THE RATE OF PHOSPHATE UPTAKE AND THE EXTERNAL CONCENTRATION

Many investigators have determined the relationship between external concentration and the absorption velocity. It was generally found that this relationship could be represented by an absorption curve of the shape of the adsorption-isotherm. For this reason, van den Honert assumed the first stage of the absorption process to consist of an adsorption process (1933, 1936).

Alberda (1948) studied this relation with high salt and low salt plants. A remarkable difference between these two types of material was that high salt plants attained their maximum rate of absorption at a lower concentration than did the low salt plants. To be able to explain this difference, Alberda assumed that, by raising the external concentration, the uptake became so large, that the transfer of phosphate into the shoots surpassed the fixation by growth. The surplus will be returned to the roots, having a damping effect on the uptake from the medium (Mason and Maskel 1931; Van de Sande Bakhuyzen 1937).

Seeing that low salt and high salt plants also differ in sugar content, these experiments were repeated. At the same time the influence of addition of sugar on this relation and on the saturation phenomenon was traced. All experiments were carried out using the root chamber (fig. 1: C). This rendered a rapid replacement of the solution possible. The sets of plants were placed on 400 or 350 cm^3 Hoagland solution of various concentrations (6·25—200 %). The p_H of the solutions was adjusted to 6·2—6·4 with sulphuric acid. To trace the effect of sugar, 2 gm glucose was added to the solutions. As a rule six different solutions, of increasing concentration, were successively applied. No essential differences were found if the solutions were applied in an inverse sequence.

The absorption periods being short, the amount of phosphate taken up was but slight. With low concentrations especially, the error of the determination of the phosphate uptake can become significant. It amounted to 0·12 mg P_2O_5/2h. at a maximum, as far as it depended on the precision of the phosphate determinations of the solutions used. At the lower concentrations it was somewhat less.

A regular periodicity of the phosphate uptake did not occur during the course of the day, but a more or less sudden change could occur. This rendered a great number of experiments necessary. In spite of this it is not possible to illustrate the regularities in the relation between concentration and uptake and the effect of glucose supplied by a single experiment.

To judge the relationship existing between the rate of uptake and the external concentration, the rates of uptake with the corresponding concentrations had to be determined. As a result of the uptake the concentration alters during the absorption period together with the rate of uptake. The velocity, obtained by analysing the solution at the start and at the end of an absorption period gives, as a matter of fact, only an average value. Now the question arises, which external concentration does this average rate of uptake belong to. As a first approximation the arithmetic mean of initial and final concentration may be used. To judge whether the points, plotted in this way, fit into an adsorption-isotherm, we can make use of the empirical formula of Freundlich:

$$u = k\,c^{\frac{1}{n}}$$

Whether the relation between the rate of uptake u and the external concentration c may be represented by Freundlich's equation can easily be seen by plotting both data logarithmically. If they satisfy this equation, a straight line will be found, for:

$$\log u = \frac{1}{n} \log c + \log k$$

The curve of the closest fit may be calculated and hence the coefficient k and the exponent $1/n$ are known and the absorption curve can be calculated and drawn.

As will appear from the experiments, the relation can certainly be represented by Freundlich's equation, at least within a certain range of concentrations. However this means at the same time that the choice of the arithmetic mean of initial and final concentration is, theoretically, not a correct one. It is possible to make an estimation of the error.

As a result of the uptake u, the concentration c of the solution falls. The intensity of this alteration depends on the volume V. The amount of phosphate absorbed during a time interval dt amounts to $u.dt$ or $k.c^{1/n}\ dt$. The resulting change of the concentration c_t can be represented by:

$$dc_t = -\frac{k.c_t^{\frac{1}{n}}}{V} \cdot dt$$

Hence:

$$dt = -\frac{V}{k} \cdot \frac{1}{c_t^{\frac{1}{n}}} \cdot d\,c_t$$

Integration gives:

$$t = -\frac{V}{k} \int \frac{1}{c_t^{\frac{1}{n}}} \cdot d\,c_t = -\frac{V}{k} \left(\frac{n}{n-1} \cdot c_t^{\frac{n-1}{n}} + C \right)$$

Assuming the initial concentration at $t = o$ to be c_o, the integration constant C follows from:

$$C = -\frac{n}{n-1}\, c_o^{\frac{n-1}{n}}$$

The relation between t and c now becomes:

$$t = \frac{V}{k} \cdot \frac{n}{n-1} \cdot \left(c_o^{\frac{n-1}{n}} - c_t^{\frac{n-1}{n}} \right)$$

The average value of the absorption velocity belongs to some concentration c, lying between c_o and c_t. The rate of uptake at this concentration is $k.c^{1/n}$. If this uptake takes place at this constant rate during the time t, a concentration decrease is obtained equal to

$c_o - c_t$, so that the formula becomes:

$$\frac{k\, c^{\frac{1}{n}}\, t}{V} = c_o - c_t$$

Hence:

$$c^{\frac{1}{n}} = \frac{c_o - c_t}{\frac{n}{n-1}\left(c_o^{\frac{n-1}{n}} - c_t^{\frac{n-1}{n}}\right)}$$

Thus it is possible to calculate the correct concentration that the average rate of uptake obtained belongs to. Meanwhile, it appeared that there was only a slight difference between this correct value of the concentration and the mean value of initial and final concentration. This was mainly due to the short absorption period, as a result of which only a slight lowering of the concentration occurred. Only with low concentrations could the mean value occasionally turn out to be a little too high. In this case the correction gave an obviously better result. As to the figures, this implied a better fitting of the points at the lower concentrations, in the absorption curve. In view of the slight significance of the correction to the result mentioned below, it was omitted. Thus all absorption rates were plotted against the mean value of initial and final concentration. The calculations were also based on these values.

From a theoretical point of view, Langmuir's equation is of more importance. As to the relation between the rate of uptake u and the external concentration c, it is given by:

$$u = \frac{k_1 c}{1 + k_2 c}$$

It follows from this equation that there is a rectilinear relationship between the reciprocal values of absorption $1/u$ and concentration $1/c$. Thus, it can easily be found how far the data are in agreement with Langmuir's equation. The constants k_1 and k_2 follow immediately from the calculation of the straight line, for:

$$\frac{1}{u} = \frac{1}{k_1} \cdot \frac{1}{c} + \frac{k_2}{k_1}$$

A formula can be derived from Langmuir's as well as from Freundlich's equation, which gives the correct concentration, to which the uptake found belongs. The result is:

$$c = \frac{c_o - c_t}{\ln c_o - \ln c}$$

where c_t and c_o again represent the concentrations at the start and at the end of the absorption period.

Of great theoretical interest is the fact, that according to Langmuir's equation, if the external concentration is increased infinitely, a "saturation value" for the rate of uptake will be obtained. This value equals k_1/k_2. It is possible by this to compare the experimental saturation value with this theoretical one in those cases where a maximum uptake was obtained.

In all experiments mentioned below, both the Freundlich and the Langmuir equations were calculated. Along with the description of a few experiments, the difference between these equation as to their ability to represent the data, will be discussed. In practical aspects Langmuir's equation is preferable because it requires far less tedious calculations. The theoretical significance of this expression will be fully demonstrated in the discussion.

Experiment 4a. This first experiment was carried out with a set of twelve old low salt plants. The plants were vigorously developed. Moreover, the absorption period lasted for three hours. An enormous uptake took place, causing a large alteration of the concentration (fig. 5: A).

During the first day four solutions of increasing concentration were tested. The relation between the rate of phosphate uptake and the mean values of initial and final concentration can be represented by a Freundlich equation ($u = 1 \cdot 71\ c^{0 \cdot 476}$) or a Langmuir equation ($u = \frac{1 \cdot 36\ c}{1 + 0 \cdot 0144 c}$). The two corresponding curves have been drawn in fig. 5: A. At the very low concentrations Freundlich's formula produces values a little higher than Langmuir's. The same applies to the high concentrations. It will be clear that it cannot be decided which curve gives the closest fit.

On the second day the experiment was repeated. Glucose was now added to every solution. There was an obvious enhancement of the phosphate absorption. An absorptive relation applied only to the first three concentrations. For this concentration range the equations give: $u = 1 \cdot 02\ c^{0,94}$, resp.: $u = \frac{0 \cdot 966\ c}{1 + 0 \cdot 0063 c}$. It follows from the high value of the exponent of Freundlich's equation, that the curve was nearly rectilinear.

The alterations of the concentrations during the absorption periods were very large. The correct concentrations were calculated together with the Langmuir equation $u = \frac{1 \cdot 252\ c}{1 + 0 \cdot 0030\ c.}$ As is shown by fig. 5: A, the error was considerable. In the other experiments this was not found, as a result of the use of a smaller number (8—10) of young plants, which were only allowed to absorb for two hours.

From the Langmuir formula the saturation value was calculated. On the first day it amounted to 94 mg P_2O_5/3h., on the second day, when glucose was added: 153 mg P_2O_5/3h., resp. 417 mg P_2O_5/3h. As a matter of fact the uptake on the second day proved to rise not above about 14 mg P_2O_5/3h. This pointed to a limiting factor.

Experiment 4b. A set consisting of young high salt plants (June 1950) was used. On the first day the uptake on a full-strength Hoagland solution during four successive absorption periods amounted to:

$$0{\cdot}34 \qquad 0{\cdot}30 \qquad 0{\cdot}42 \qquad 0{\cdot}30 \text{ mg } P_2O_5/2\text{h}.$$

This variability falls within the error of the phosphate determinations.

On the second day the uptake on six solutions of increasing concentration was studied (fig. 5: B). During the fourth absorption period aeration was insufficient. The immediate depressing effect on the uptake was striking. During the fifth period the uptake had not yet attained its original rate. It is not very likely that the uptake would have been much higher during the sixth period, in view of the absorption rates found the next day. For the three lower concentrations we obtained: $u = 0{\cdot}097 \ c^{0{\cdot}715}$, resp. $u = \dfrac{0{\cdot}0685\, c}{1 + 0{\cdot}0336\, c}$. From the last expression a saturation value follows: 2·3 mg P_2O_5/2h. The maximum rate obtained was ± 0·95 mg P_2O_5/2h. that was already attained at a concentration of 24 mg P_2O_5/l.

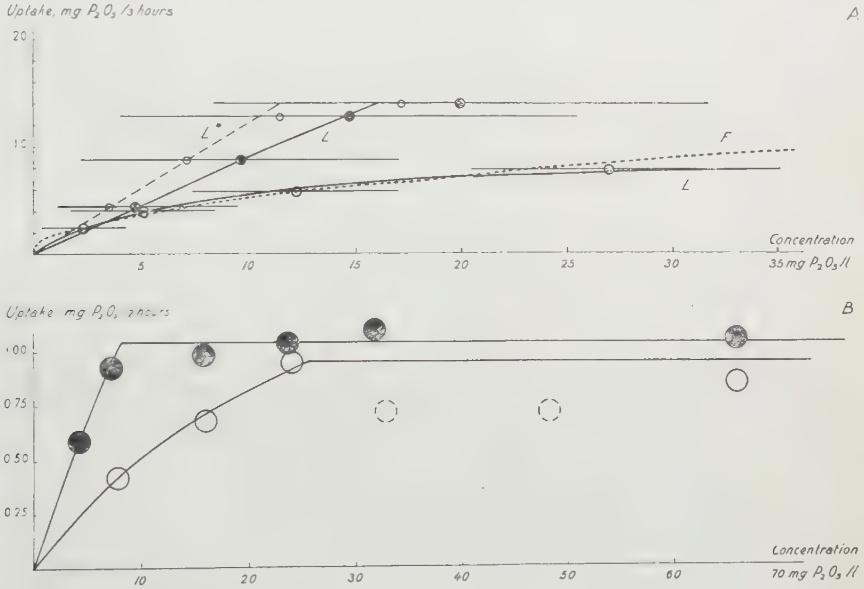


Fig. 5. The relation between the rate of the phosphate uptake and the external concentration, before (o—o) and after (●—●) glucose addition. A: by a set of large low salt plants; B: by a set of high salt plants. F: Freundlich curve; L: Langmuir curve; L*: corrected Langmuir curve, belonging to corrected concentration values.

The next day glucose was added to the solutions. For the two lower concentrations we obtained: $u = 0 \cdot 182\, c^{0 \cdot 829}$, resp.: $u = \frac{0 \cdot 162\, c}{1 + 0 \cdot 0316\, c.}$ In this case also, the relation was almost rectilinear after the addition of glucose. The saturation value was also much larger viz. 51·3 mg P_2O_5/2h. The uptake was found not to increase in practice any longer above a concentration of 8 mg P_2O_5/1. It did not differ significantly from the maximum rate of uptake the day before, when no glucose was administered. Hence, by addition of glucose the amount of phosphate that can be utilized maximally by the plant was not increased, although the ease with which phospate can be taken up from the external solution was increased.

Experiment 4c. This experiment was performed with a high salt and a low salt set, grown under very favourable conditions (July—August 1951). During the first two weeks of cultivation both sets received a high salt treatment. Then the low salt set was put on tap water, the solution of the high salt set being renewed every other day. After one and a half week the sets were used for the experiment. They were brought into the room of constant temperature under an intensive illumination. The day before the experiment was started, the high salt set was placed in darkness to reduce the sugar content as much as possible. During the first three days of the experiment the low salt set continued to be in the light and the high salt set to be in darkness. Figure 6: A represents the relation between the uptake and the concentration of the low salt set on the first day. The seven solutions were applied with increasing concentrations. There was a regular increase of the uptake ($u = 0 \cdot 273\, c^{0 \cdot 384}$, resp. $u = \frac{0 \cdot 432\, c}{1 + 0 \cdot 502\, c}$). Quite a different result was obtained with the high salt set on this day (fig. 6: B). At low concentrations the uptake rose with increasing concentrations ($u = 0 \cdot 471\, c^{0 \cdot 341}$, resp. $u = \frac{0 \cdot 632\, c}{1 + 0 \cdot 516\, c}$). But at a concentration of about 14 mg P_2O_5/1. the maximum rate of uptake was attained. At higher concentrations the uptake remained 1·12 mg P_2O_5/2h. The theoretical value derived from the Langmuir's equation, amounted to 1·22 mg P_2O_5/2h.

The next day this experiment was repeated. Higher concentrations up to 66 mg P_2O_5/1. were used. They were used in decreasing concentrations. Fig. 6: C and D represent the results (the absorption values at the higher concentrations have been omitted, in order to bring the figure into accord with the other ones). With the low salt set the uptake was again found to increase over the whole range of concentrations used ($u = 0 \cdot 457\, c^{0 \cdot 252}$). The rates were rather higher than they were on the first day. At the lowest concentrations the values were even higher than could be expected theoretically. This could be explained by assuming an increase in the absorption activity during the last two absorption periods on this day. For on the next day the uptake proved to be much higher than it was on the previous days.

The result for the high salt set on the second day was quite different to what it was on the first day (fig. 6: D). The absorption velocity was greatly decreased. Moreover, there was no maximum uptake. At the highest concentration (66 mg P_2O_5/l.) the rate of uptake was 1·06 mg P_2O_5/2h. (not represented by the figure). This equalled the maximum rate of the first day. Hence, the rate was not very likely to increase with still higher concentrations. Thus, by a prolonged stay in the darkness the maximum amount of phosphate was not diminished but the ease with which phosphate could be absorbed from low external concentrations was ($u = 0 \cdot 107\, c^{0 \cdot 542}$, resp. $u = \frac{0 \cdot 0765\, c}{1 + 0 \cdot 0812\, c}$). The efficiency of the absorption mechanism was diminished. The theoretical saturation value had also been lowered only little, it amounted to 0·94 mg P_2O_5/2h.

On the third day the influence of the addition of glucose was traced. As a check, the uptake was first determined on a Hoagland solution without glucose. After this the sets were placed on a solution of the same concentration to which glucose was added. Then four more solutions of decreasing concentrations, also with glucose, were used.

The uptake of the low salt plants (fig. 6: E) was much higher than it was the days before ($u = 1 \cdot 002\, c^{0 \cdot 179}$, resp. $u = \frac{1 \cdot 518\, c}{1 + 0 \cdot 849\, c}$). However, as will appear from a comparison with the control, this enhancement was not the result of the sugar supply. It must be due to a normal increase in the absorption activity of the low salt plants (see irregularities at the end of the second day). It is remarkable that this increase was obtained at all concentrations. The ratio between the rates of uptake on this day and the rate on the first day follows from the Freundlich equations. It amounts to $3 \cdot 7\, c^{-0 \cdot 2}$. This means that the lower the concentration the higher this ratio: i.e. the enhancement of the uptake. The absorption mechanism had become more efficient. This follows immediately from the falling values of the exponents of the Freundlich equations (0·384, 0·252, 0·179). From the Langmuir equations it can be seen that the saturation values were also raised (up to 1·78 mg P_2O_5/2h.).

With the high salt set the effect of the glucose supply was obvious (fig. 6: F). The effect increased during the course of the day and especially during the second part. The result was an irregular relationship between the concentration and the uptake: the uptake at a lower but later applied concentration could be higher. It is difficult to give the theoretical relationship but rather arbitrarily it is indicated in two ways viz. for the uptake at the higher concentrations (curve *a*) and for the uptake at the lower concentrations (curve *b*). The Freundlich equations were: $u = 0 \cdot 127\, c^{0 \cdot 608}$, resp. $u = 0 \cdot 633\, c^{0 \cdot 349}$.

The uptake without glucose at a concentration of ± 32 mg P_2O_5/l. was not significantly different from that of the previous day, so a continued decrease as a result of the dark treatment had not occurred.

Therefore, the relationship between the uptake and concentration may be assumed not to be changed very much, so that it can be represented approximately by the same curve (curve *c*). It appears from a comparison of curves *a* and *c* that by the addition of glucose the uptake was enhanced. The enhancement gradually decreased with the external concentration. The same result was obtained with experiment 4a and 4b (fig. 5). The Freundlich line was less curved.

Quite different conclusion can be derived from a comparison of curves *b* and *c*. The enhancement was much higher. This result can be compared with that of the low salt set of this experiment (a stronger curvature of the Freundlich line). The conclusion seems to be justified that the glucose had a complex influence on the phosphate uptake. How far the occurrence of the secondary effect (which was not obtained in the previous experiments) was connected with the different sequence in which the concentrations were used needs further examination. At any rate, the high salt plants showed a decrease of absorption in the darkness, especially at the lower concentrations. Probably the maximum uptake possible did not change very much. The uptake was enhanced by sugar supply. The effect increased during the course of the day.

At the end of these first three days of the experiment the low salt set was placed in the dark, the high salt set in the light. The nutrient solution of the latter set was renewed daily; the former one was put on tap water. This treatment lasted for three days. Then, on the sixth and seventh day of the experiment, the relation between uptake and concentration was once more determined; on the sixth day without and on the seventh day with addition of glucose.

Figure 6: G shows the result of the low salt set without glucose ($u = 0 \cdot 466\, c^{0 \cdot 325}$). The relationship between the concentration and uptake was virtually similar to that of the first day. The rates at all concentrations were 1·7—1·8 times those of the first day. There was a slight irregularity in the rate of uptake at 17 mg P_2O_5/l. which was a little higher than could be expected. The Langmuir curve ($u = \frac{0 \cdot 346\, c}{1 + 0 \cdot 224\, c}$) fitted much closer to the data than did the Freundlich curve. The theoretical saturation value was 1·54 mg P_2O_5/2h. Thus this showed a decline.

The result of the high salt set was more irregular, because of the increase in absorption activity during the course of the day. During the first three absorption periods the uptake rose in spite of the decreasing concentration. Figure 6: H shows the relation for the lower four concentrations ($u = 0 \cdot 941\, c^{0 \cdot 310}$). The maximum rate of uptake found (2·15 mg P_2O_5/2h). was attained at a concentration of 14·5 mg P_2O_5/l. This was very likely to be the highest possible uptake, as can be seen from a comparison with the results of the next day.

The addition of glucose had a very strong effect with the low salt set (fig. 6: *I*). The uptake had become very low as a result of the dark treatment (0·6 mg instead of 1·4 mg P_2O_5/2h.). The increase

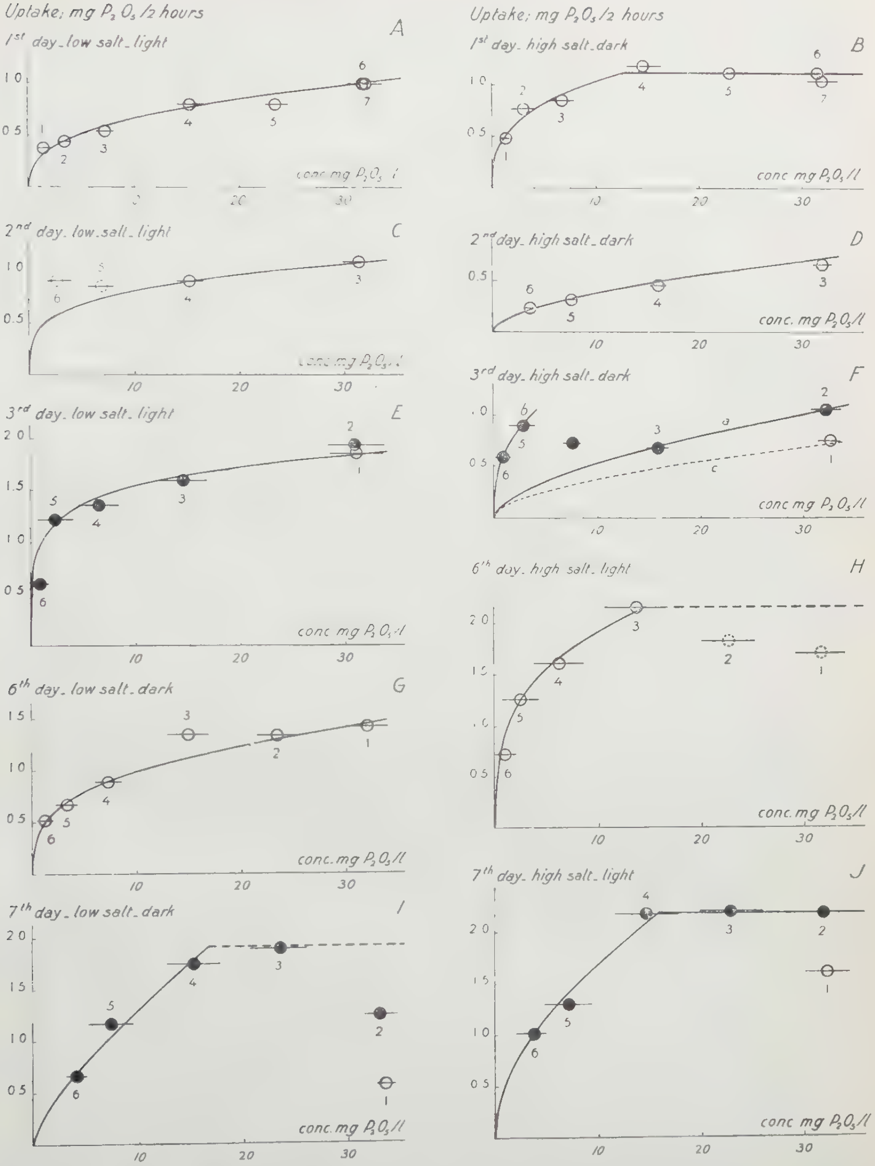


Fig. 6. The relation between the rate of the phosphate uptake and the external concentration with high salt and low salt plants, in light and darkness without (o—o) and with (●—●) glucose addition. In all graphs, Freundlich curves have been drawn.

of the uptake due to the glucose addition, increased during the first absorption periods. During the second part of the day a normal relationship was found ($u = 0 \cdot 259\, c^{0 \cdot 714}$).

The results obtained with the low salt set were according to expectations. It could not be established whether there is a maximum rate of uptake within the range of concentrations used. The influence of the glucose increased during the course of the day, as had been the case with the high salt set in darkness (fig. 6: F).

The uptake of the high salt set was on the last day less than on the previous day. The uptake increased after glucose had been added. At lower concentrations the equations were: $u = 0 \cdot 497\, c^{0 \cdot 537}$ and $u = \frac{0 \cdot 420\, c}{1 + 0 \cdot 151\, c}$.

A maximum absorption rate of 2·19 mg P_2O_5/2h. was attained. It amounted to 2·15 mg P_2O_5/2h. on the previous day. So it was not increased significantly. In experiment *4b.* also the maximum uptake was found only to change little, the uptake at the lower concentrations being markedly enhanced. Moreover, in both cases the Freundlich curve was more rectilinear.

The data of the last two days showed that the rate of uptake was much higher than it had become during the first days of the experiment as a result of the dark treatment. At the same time the saturation phenomenon, that had disappeared during the dark treatment, returned.

Experiment 4d. In this experiment a set of high salt plants was used, grown under very favourable conditions of light and temperature (July—August 1950). As a result the plants were well developed and their uptake was high. During the experiment the plants were intensively illuminated.

On the first day the uptake was determined for six increasing concentrations. On the second day this was repeated, 2 gm glucose being added to the solutions. As figure 7: A shows, the uptake was the same over the whole range of concentrations on both days ($u = 3 \cdot 33\, c^{0 \cdot 190}$). The uptake rates were large, particularly at the low concentrations (where the absorption curve is very much curved), as is expressed quantitatively by the low value of the exponent of c, viz. 0·190. A simular result was obtained in the previous experiment in those cases where the absorption activity, also without sugar supply, was high. The fact that glucose had no effect, indicated that the plants were in a high sugar condition. The absence of a maximum absorption rate is particularly striking, though very high concentrations were used. Thus there was no limiting factor with these rapidly growing plants.

Figure 7: A also shows the Langmuir curve ($u = \frac{1 \cdot 692\, c}{1 + 0 \cdot 230\, c}$). Its closer fit to the data, especially at the lower concentrations, is remarkable. This was a normal result with plants showing a high

absorption rate also at low concentrations. This is connected with an essential difference between the two types of curves. The curvature of the Freundlich curve continues to increase with lower concentrations. It attains its maximum at $c = o$. This does not apply to Langmuir's equation. The concentration at which its curvature is highest, follows from: $c = (k_1 - 1)/k_2$. Depending on the value of k_1, this concentration may be either negative, zero or positive. The last possibility is significant as it gives a picture differing from Freundlich's curve. In figure 7: A the Langmuir curve shows its highest curvature (for the given method of plotting) at 7·0 mg P_2O_5/l. The relationship is more rectilinear below this value as well as above this value. In principal by experiments such as this one, a decision is rendered possible as to which equation, Freundlich's or Langmuir's, gives the closest fit to the data.

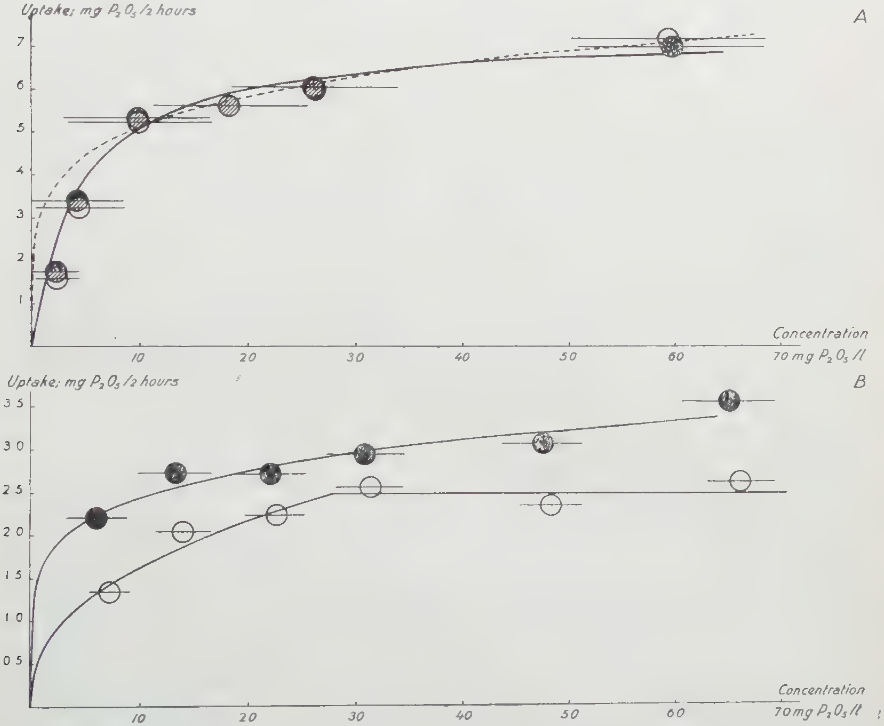


Fig. 7. The relation between the rate of the phosphate uptake and the external concentration before (o—o) and after (●—●) glucose addition. A: high salt plants; B: low salt plants.

Experiment 4e. A few weeks after the previous experiment a similar experiment was carried out with a low salt set. The results are represented by figure 7: B. Solutions were applied with increasing concentrations, on the first day without and on the second day with glucose. The uptake seemed to be stimulated by glucose addition.

But it is quite possible that it was the normal increase of absorption activity as had been generally found with low salt material (e.g. experiment 4*c*; fig. 6: E). Moreover, sugar supply was not very likely to be a limiting factor with low salt plants, which normally are in a high sugar condition. The most striking result was the finding of a concentration above which there was no further increase of the phosphate uptake. This result was no longer obtained on the second day, when the absorption activity had been increased. This suggests that the saturation phenomenon on the first day was due to some physiological factor allowing only a restricted uptake. This limitation was removed the next day. This renders the factor likely to be connected with the low salt condition. The most striking feature of the low salt plants, in contrast with the high salt ones, was their inhibited growth particularly in the shoot. Hence, as a preliminary explanation of the saturation effect, the limiting influence of the growth, due to the low salt condition, may be used.

The Langmuir equations were on the two consecutive days: $u = \frac{0 \cdot 327\, c}{1 + 0 \cdot 097\, c}$ and $u = \frac{1 \cdot 033\, c}{1 + 0 \cdot 310\, c}$. From these the saturation value can be derived: 3·40 mg and 3·33 mg P_2O_5/2h. No change of this value had occurred. But whereas this value was indeed attained on the second day at the highest concentration used, this did not happen on the first day. This pointed once more to the omitting of a limiting factor.

The concentrations at which the Langmuir line was most curved, were 6·4 and 6·0 mg P_2O_5/1. No absorption value being available at concentrations below these values, it was not possible to judge whether these curves gave a closer fit than the Freundlich curves.

Discussion

If no irregularities occurred, the absorption curve, representing the relation between the rate of phosphate uptake and the phosphate concentration of the medium, was always found to have the appearance of an adsorption-isotherm. Sometimes this applied to the whole range of concentrations used (up to 60—70 mg P_2O_5/1.). Sometimes a maximum rate was already attained at a lower concentration. This "saturation phenomenon" is quite a normal one with ordinary adsorption processes. Therefore, the conclusion seems to be legitimate that, as Van den Honert expounded, the first stage of the uptake consists of an adsorption process, by which equilibrium is rapidly established. The ions adsorbed in this way have to be transported further at a constant velocity. Therefore, to the whole process of uptake the picture of the conveyor belt can be applied.

But, though the general relation between concentration and uptake becomes understandable in this way, it is not possible to explain all the facts obtained in these experiments. For instance it was found that glucose supply enhanced the uptake. This might be explained by assuming the glucose to be partly phosphorylated. However it is then difficult to see why the relationship between the concentration and the resulting uptake (now consisting of the normal uptake and the utilization by phosporylation) has again an adsorptive nature. Also the fact, that sometimes no influence at all was found of the glucose supply at the higher concentrations, speaks against this assumption. It must be assumed that the normal uptake has been increased. To use the picture of the conveyor belt: either the loading of the belt or the rotation velocity has been altered. It is obvious first to think of the rotation velocity, as it is closely connected with metabolism. But if this is correct, the uptake can be expected to be enhanced relatively to the same extent at every concentration. The relation between uptake and concentration being represented by $u = k.c^{1/n}$, only a change of k can be expected as a result of the addition of sugar. Such an alteration of the relation was found by van den Honert as to the influence of temperature. Moreover as far as a maximum rate of uptake had occurred, this should have been found to happen at the same concentration.

As a matter of fact the uptake was always found to change in a different extent at different concentrations. Such a change not only occurred as a result of glucose addition. By a dark treatment the uptake was diminished especially at the lower concentrations. Low salt plants showed an increase in the absorption activity during the first days of the experiments. This increase happened again mainly at the lower concentrations. On the other hand, if the uptake was enhanced by glucose addition, the higher concentrations were favoured. The relation became nearly rectilinear.

This means it had to be assumed that the first stage of the uptake: the "adsorption" (the loading of the conveyor belt) can be changed too e.g. by glucose addition. This consideration can easily lead to the hypothesis that this first stage involves a formation of hexosephosphate. At any rate, the experiments with phloridzin pointed to the fact that phosphorylations are significant in the uptake of phosphate. If this hypothesis is correct, it means that the first stage of the phosphate absorption by plant roots is enzymatic in nature. For many enzymatic processes it is known that the relation between the reaction velocity and substrate concentration can be represented by a Langmuir equation. This is explained by the theory of MICHAELIS and MENTEN (HÖBER 1945; SCHWAB 1941).

The hypothesis, that the phosphate uptake begins with the formation of a hexose phosphate, was the very starting point of the exposition given below. Meanwhile, this hypothesis did not prove to be a necessary condition to give an explanation of the phenomena obtained. For this it is sufficient to generalize the picture of the conveyor-belt followed till now. Meanwhile, the strong resemblance between the Langmuir treatment and the Michaelis-Menten formulation of enzyme kinetics is evident from this (BULL 1951). This need not surprise us since the Langmuir equation has a very general form so that it applies to various processes and reactions (HINSHELWOOD 1946). For a critical discussion of the principles, involved in catenary processes and limiting factors, reference may be made to an excellent survey of BOOY and WOLVEKAMP (1944).

Phosphate P, present in the medium, is assumed to be bound in a reversible way to a substance X, which is present in the symplasm of the root only in a limited amount. This process can be represented by:

$$P + X \underset{k''}{\overset{k'}{\rightleftarrows}} PX$$

It should be added that this representation may be a simplified expression of a more complicated chain of reactions. The "velocity constants" k' and k'' may appear to depend on many factors e.g. on the sugar metabolism. Moreover X may also represent some protoplasmic particle.

Secondly phosphate must be transferred at a constant rate. It may be that the complex PX is immediately broken down. However, it is equally probable that phosphate is transferred as PX and that the decomposition occurs after some time. In both cases some X becomes again available for binding phosphate of the external solution. Attention should be drawn to the fact that phosphate can be liberated from PX into the medium as well as into the symplasm of the root. The former process will be referred to as dissociation of PX. The latter process constitutes the uptake and will be referred to as transfer of phosphate. The rate of this transfer (it is the rotation velocity of the conveyor belt) can be expected to be dependent on the glucose concentration. As to the velocity u with which phosphate is absorbed:

$$u = k\, c_{PX} \cdot c_G$$

now applies, where c_{PX} and c_G represent the concentrations of the compound PX and of glucose.

During a steady state the concentration c_{PX} has a constant value. The velocity with which the compound is formed then equals the velocity with which it is broken down by dissociation and transfer. Hence:

$$k' c_P c_X = k'' c_{PX} + k\, c_G c_{PX}$$

If the total available amount of the substance X equals C, so that:

$$C = c_X + c_{PX}$$

the concentration of PX can be derived from the two last formulae:

$$c_{PX} = \frac{k' C\, c_P}{k'' + k\, c_G + k' c_P}$$

Substitution of this value of c_{PX} in formula concerning the absorption rate gives finally:

$$u = k' C\, k\, c_G \frac{c_P}{k'' + k\, c_G + k' c_P}$$

This expression can easily be written in the general form of Langmuir's equation:

$$u = \frac{k_1\, c_P}{1 + k_2\, c_P}$$

if:

$$k_1 = \frac{k\, k'\, c_G\, C}{k'' + k\, c_G} \quad \text{and} \quad k_2 = \frac{k'}{k'' + k\, c_G}$$

The maximum possible rate of uptake k_1/k_2 now tends to $k\ c_G\ C$ This could be expected, since this rate of uptake only occurs if the whole available amount of substance X is continuously bound to phosphate, so that c_{PX} equals C. This saturation value is always proportional to C. The same applies to the absorption velocity at lower concentrations. However, the glucose concentration has quite another influence. The uptake is increased by glucose addition, it is true, but the extent to which this happens depends on the external phosphate concentration. This can be illustrated most clearly by considering two extreme cases, each of which can be represented by a more simple expression.

In the first place the transfer of phosphate $(= k\ c_G c_{PX})$ can be supposed to be negligible compared with the dissociation velocity of this compound $(= k'' c_{PX})$. Then $k c_G \ll k''$ and the formula becomes:

$$u = k\, \frac{k'}{k''} \cdot c_G \cdot C\, \frac{c_P}{1 + \frac{k'}{k''}\, c_P}$$

Increasing the glucose concentration has the same effect that increasing the X concentration has viz. the same enhancement at all phosphate concentrations. It produces the same result that could be expected on the grounds of the initial theoretical considerations. This is understandable, for these considerations lead to the same equation. For if the first stage of the uptake consists of an adsorption, the equilibrium of which is established very rapidly compared with the rate of further transport, the "loading of the conveyor belt" is given by:

$$c_{PX} = \frac{k'}{k''} \cdot C\, \frac{c_P}{1 + \frac{k'}{k''} \cdot c_P}$$

if Langmuir's derivation is used. Now C represents the total quantity of adsorption-points, c_{PX} the concentration of the points occupied by phosphate ions. In order to obtain the formula for the uptake, the expression needs only to be multiplied by $k\ c_G$; i.e. the rotation velocity of the conveyor-belt.

The second extreme case occurs if the dissociation velocity of PX is low compared with the velocity at which phosphate is transferred

$(k'' \langle\langle k\, c_G)$. The formula can be simplified to:

$$u = k' C \frac{c_P}{1 + \frac{k'}{k'' c_G} \cdot c_P}$$

Increasing the glucose concentration involves also in this case an enhanced phosphate uptake. This enhancement is however different at different concentrations. The range of concentrations over which the uptake is nearly linearly proportional to the external phosphate concentration becomes much larger after glucose addition. This is more in agreement with the experimental results. With glucose the relation between uptake and concentration was virtually rectilinear; this was clearly demonstrated by the high value of the exponent of the Freundlich equations.

This second case fits more closely to the data. But this does not mean, that the extreme conditions of this case were always fulfilled. The result indicated will also be obtained with less extreme conditions, viz. as long as the absorption velocity of phosphate remains a non-negligible factor compared with the dissociation velocity of the complex *PX*.

As a starting point for the foundation of this theory the hypothesis was used that phosphate was bound initially to glucose. It will be clear that the proposition, just given, can be applied to this case unaltered. The role of the substance *X* can be played by either some enzym or some intermediate product produced at the formation of hexose phosphate. It is tempting to think particularly of the energy-rich phosphorus compounds. By this the results with low salt material might be partly explained. For, by supplying phosphate during the experiments they are allowed to enlarge their adenyl acid-complex. By this the phosphate uptake might be enhanced immediately. Moreover, the check on the development of the plants might be abolished and this will have a secondary effect on the phosphate uptake i.e. by removing the limiting effect of growth on the uptake at high concentrations.

Attractive as this hypothesis may be from a biochemical point of view, the general concept should be preferred for the present. A further elaboration needs more biochemical examination. A great advantage of the exposition as given here, is that it can be applied to other ions. It may be considered therefore, a quantitative elaboration of those theories in which ions are assumed to be bound to carriers.

If the explanation given is correct, Langmuir's equation proves to be of particular significance. It may be used in calculating the maximum uptake (the "saturation" value). This is of primary importance to those experiments in which a concentration was found above which the uptake did not increase any longer. Summarizing the following results were obtained:

Experiment	Treatment	Maximum uptake	
		theoretical	experimental
fig. 6: B, H, J high salt	darkness	1·22	1·12
	light	2·39	2·15
	light + glucose	2·78	2·19
fig. 5: A high salt	light	2·30	1·00
	light + glucose	51·3	1·04
fig. 7: B low salt	light	3·40	2·48

In the experiments with high salt material as a rule a maximum was found. Only as a result of a prolonged dark treatment was the uptake decreased and did the "saturation phenomenon" disappear. As is clear from the table, this experimental maximum level was mostly lower than the theoretical one. This means that there was another process, that may have a limiting effect on the uptake. The sugar supply might be supposed to be this limiting factor. This is disproved by the experimental data. By sugar addition the maximum uptake was not increased, although the uptake at lower concentrations was. A much higher uptake should have been expected, if the limitation was the result of a "saturation".

If neither the phosphate concentration nor the glucose supply can be the check on further increases of the phosphate supply, this check has to be sought in the further utilization of phosphate in the plant. With high salt plants the ability to accumulate ions in the vacuoles is but slight in contrast with low salt plants. This renders it intelligible why a maximum uptake is so often found with high salt plants. A more important factor than the vacuole accumulation is perhaps formed by the consumption of phosphate by growth processes.

In the experiments last mentioned in the table, glucose addition did not change the maximum absorption rate. This would mean that the growth processes were not enhanced by the glucose, but the phosphate uptake was, at least at low concentrations. On the other hand, with experiment 4*c* (fig. 6: F) clear secondary effects were observed on plants which had been in darkness for some days. Whether the maximum uptake was also increased by adding glucose, could not be affirmed. Meanwhile it will be clear that glucose may have a complex influence.

With low salt plants it was observed only once, that the uptake was limited at high concentrations in the same way as it was with high salt plants. This happened only on the first day of the experiment. At that time the development of the plants was as yet much inhibited by a phosphorus deficiency. Thus a limiting influence of the growth can also explain the "saturation phenomenon" in this case.

This "saturation phenomenon" has been the very starting point of this investigation into the relation between the phosphate uptake and the external phosphate concentration. An attempt was made to study the influence of glucose on this maximum value in detail. Indications were obtained that it is possible to influence this phenomenon. It was assumed that this was due to a glucose effect on growth processes. How far the hypothesis is correct that there may be, in general, a regulating influence of utilization on uptake, will be discussed in the next section, on the basis of experiments specially planned with this problem in mind.

5. THE DIRECT INFLUENCE OF THE UTILIZATION ON THE UPTAKE OF NITRATE

In the preceding chapters the growth was occasionally supposed to be a regulating factor on the phosphate absorption. Along this line of thought moved ALBERDA and VAN ANDEL, ARISZ and HELDER (1950). Starting from the assumption that high salt material is saturated with salt, it seems to be imperative that there must be growth before any uptake can occur. Also among the literature, particularly in old physiological and agronomical papers, the conception is met with of a regulating influence of the utilization on the uptake (SACHS 1874; PFEFFER 1897; NELSON 1946; WILLIAMS 1948), as was discussed in detail by the author. (HELDER 1951) This idea is mainly supported by the frequent appearance of a correlation between growth and absorption activity (STEWARD 1935). There are however many factors by which the uptake is determined. In the case of the uptake of phosphate, the concentration of the medium, as well as the sugar supply, proved to be of great significance. Hence it is not entirely excluded beforehand that the uptake should be determined by these factors. Likewise a slight growth capacity could go together with a low content of sugar, which should mean a small uptake at the same time. It is true, it was rendered likely in the previous section that concentration and sugar supply are not the only determining factors, but the principal possibility obviously illustrates that the significance of the growth for the uptake is not so self-evident as is usually accepted. Moreover it follows that only by a direct causal analysis can it be settled how far the correlation between growth and uptake is the result of a determining influence of the growth on the uptake. This means in the first place that the plant material has to be in a condition at which a regulating influence of the growth on the uptake can be expected. The plants were therefore brought into a high salt condition. In the second place with this material it must be possible to regulate the growth. This was attempted with the aid of indole acetic acid, which was added to the nutrient solution. This had no effect however. Only at the highest possible concentration was the phosphate uptake inhibited (SCHUFFELEN 1948). But then clearly damage occurred: the solutions were brown in colour at the end of the absorption period. In view of the results obtained, this negative result is not surprising. For, by this growth substance, in the first place the extension growth is inhibited. As we shall see it is rather the protoplasmic synthesis that is connected with the uptake of anions.

Following on a suggestion from Prof. Dr W. H. Arisz, use was made of the inhibiting effect of a lack of nitrogen or phosphorus on the growth. For this purpose an orientating experiment was made (1949) in which plant material was grown on a Hoagland solution, without nitrate or without phosphate. After about four weeks the plants were placed on a full-strength nutrient solution and the uptake of the phosphate, resp. the nitrate was determined. This experiment was performed under glasshouse conditions. As a result of this the course of the uptake was irregular. In spite of this there was an enhancement of the uptake of the nitrate owing to the addition of phosphate with the low phosphate sets within two days.

As, in the first place we were concerned with the principle of a regulating influence of the growth on the anion absorption, the definitive experiments of 1950 were performed with high nitrate, low phosphate material. In the first experiment the effect of administration of different quantities of phosphate on the growth and the uptake of nitrate was investigated. In the second experiment the number of treatments was enlarged and amongst others, phosphate was withheld once more and the effect was studied. With the nitrate absorption by high nitrate- low phosphate plants a result was more easily attained than with phosphate absorption by high phosphate-low nitrate material; this may be the result of a combination of two circumstances. In the first place nitrate is consumed by the growth processes (synthesis of proteins) to a greater degree than is phosphate. In the second place various phosphorus compounds of the cytoplasm have a more regulating influence on the metabolism than have the nitrogen compounds. In spite of this it must be possible to find some effect of the nitrate on the phosphate absorption with the right treatments and under the right conditions. And as a matter of fact Scott Russell and his collaborators seem to have obtained results with this tendency (personal communication).

Experiment 5a. The first experiment was performed with six sets of plants grown in June 1950. The six sets were divided into three groups (fig. 8: I, II and III). The plants were illuminated continuously. During the first two days the three sets remained on a solution without phosphate, the solution being renewed every day. Growth was slightly enhanced, probably due to the favourable circumstances in the room of constant temperature, since it was found that if this treatment was continued (fig. 8: A I) the development of the shoot gradually decreased; the increase in length as well as the number of young leaves appearing, decreased more and more. If however, only a small amount of phosphate (6.5 mg per day) was added, this decrease did not occur. The increase in length as well as the number of young leaves appearing remained more or less at a constant level (fig. 8: A II). A yet more vigorous development could be obtained by putting the plants (fig. 8: A III) on a solution with the normal amount of phosphate (a complete Hoagland solution).

At the end of the experiment phosphate was also supplied to the first set, which gave a striking effect: a rise in the increase of length and suddenly a larger number of new leaves appearing. The differences in development of the shoot due to the differences in amount of phosphate applied, were much more striking than could be represented by the figure. It was already possible to distinguish on the 4th—5th day (that is 2 or 3 days after applying phosphate) the three groups by sight. The more phosphate that was administered the more vigorously were the shoots developed, while the colour changed from the dark green of plants with phosphate deficiency to a more yellow-green.

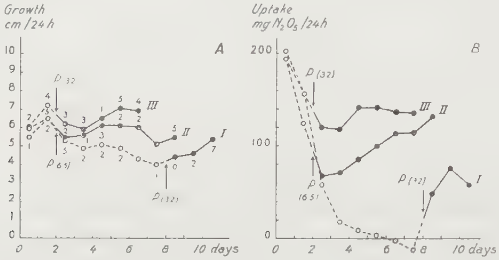


Fig. 8. The influence of phosphorus supply on the growth of the shoots (A) and the nitrogen absorption (B) of three sets (I, II, III) of phosphorus deficient maize plants. The curves are dotted during the time the plants were standing on a solution without phosphate. P (6,5) and P (32) refer to the amounts of phosphorus (mg. P_2O_5/l.) present in the nutrient solution. The growth is represented by the average increase in length of the youngest visible leaves and the number of new leaves appearing.

Quite the same but more striking results were obtained with the nitrate absorption. If no phosphate was supplied, there was a continuous fall in the rate of uptake, which came to a standstill after about five days (fig. 8: B I). If however, a small amount of phosphate was added to the solution each day, this fall was reversed, with some retardation, into a gradual increase of the rate of uptake. At the end of the experiment about the same level was reached as that of the third set, to which the normal amount of phosphate was supplied. With this set there was already some effect on the first day; then there was a slight rise up to a more or less constant level. Again a striking effect was obtained by phosphate supply with set I at the end of the experiment.

Owing to the low phosphate condition of the plants and the favourable conditions, a strong absorption of the phosphate occurred. During the first days the solution was completely exhausted. Thus the phosphate (0, 6·5 and 32 mg) added to enhance the growth was completely taken up. Only with the third set did a small amount of phosphate (about 1 gm) remain in the solution on the fourth and fifth day.

By this experiment the inhibiting effect of phosphorus deficiency on growth as well as on nitrate absorption was clearly illustrated.

By means of supplying phosphate this decline in both processes was immediately changed into an increase.

Experiment 5b. This experiment was performed with four sets of plants which were also in a high nitrate- low phosphate condition. Moreover two sets were examined, which were in a complete low salt condition (August 1950). The results are shown by fig. 9. Each of the separate graphic representations corresponds to one of the six sets used. By this the irregularities, particularly those of the growth are rather more large than in the former experiment, where the means of two sets were represented. The plants were illuminated for 16 hours every day.

There were three periods of four days during this experiment; each period being characterized by a certain treatment. During the first period all high nitrate sets (fig. 9: A, B, C, D) were on a Hoagland solution without phosphate. There was again a slight decrease in the growth but an obvious effect on the uptake; at the end of this period the absorption had almost come to a standstill.

Set A was hereafter placed on tap water and then for another period of four days once more on a solution without phosphate. So this set had not been able to absorb any phosphate from the medium either during the pretreatment or during the experiment itself. The depressing influence of the phosphate deficiency on the growth was clearly shown by the continuous decrease in the development of the shoot.

As to the nitrate absorption, during the tap water period no uptake could take place of course, but if then the plants were again put on a solution with nitrate, a renewed though small uptake appeared in spite of the fact that no phosphorus had been taken up. The amounts of nitrate taken up in this last period, are too large and the uptake goes on too long for this uptake to be due to an exchange. In this connection it may be recalled that the nutrient solutions were made with tap water. It can be concluded, that the standing still of the uptake at the end of the first period is not due to a direct depressing influence on the absorption mechanism, but rather to a nitrate saturated condition of the material. If only a slight growth had taken place, some uptake was again possible.

Quite another picture was obtained if a small quantity of phosphate was supplied (fig. 9: B). Compared with A, growth was only a little promoted; at the same time uptake started again and gradually increased. If phosphate was withheld once more, the development of the shoot diminished. Although the uptake of nitrogen went on for another two days, this was followed by a rapid fall. It could be proved by supplying some phosphate after this third period, that this fall was a consequence of lack of phosphorus. A rapid rise in the nitrogen uptake was then obtained (not reproduced in fig. 9: B).

If the amount of phosphate was increased to the normal level, stronger effects were obtained (fig. 9: C). There also was a vigorous further development during the third period, when phosphate was again withheld. The uptake rose at once to a more or less constant level. During the third period the uptake even increased a little, the cause of this is not quite clear. Perhaps it was only an after-effect of the abundant phosphate supply. At any rate there was no fall as with the former set. The amount of phosphate supplied had evidently been sufficient for a vigorous further development.

Phosphate was also supplied to the last high nitrate set but at the

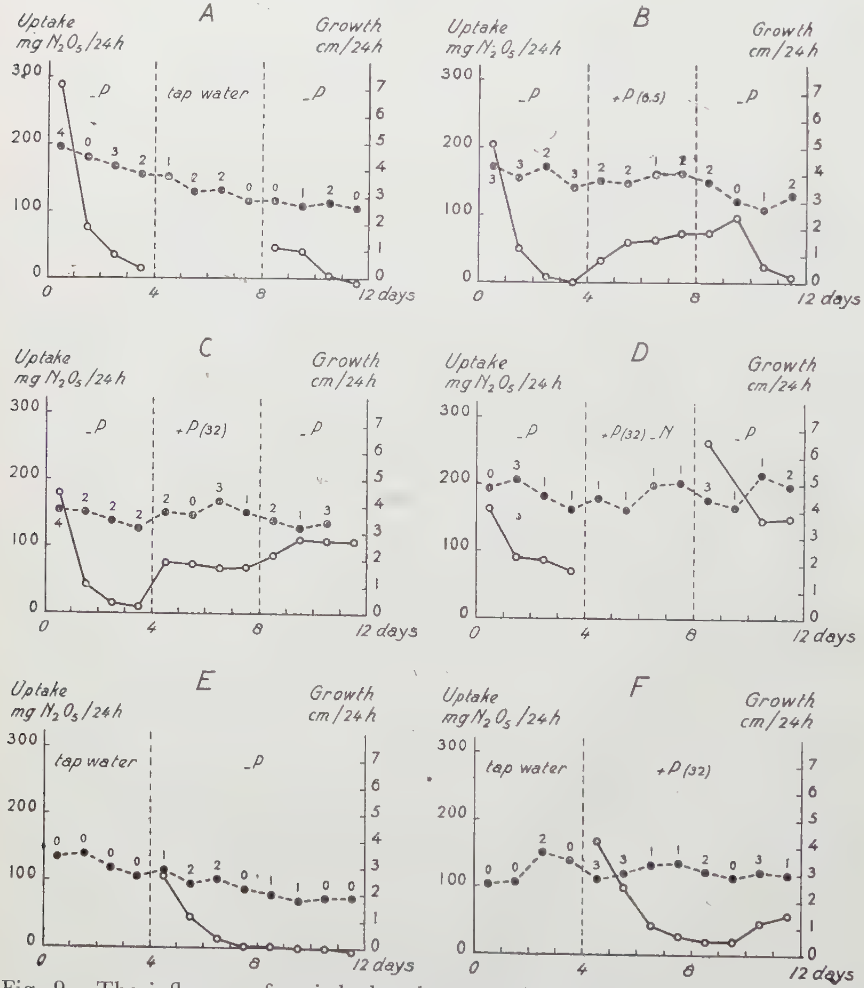


Fig. 9. The influence of varied phosphate supply on the growth (— — — —) and the nitrogen absorption (————————) of maize plants. Set A, B, C, and D were at the start of the experiment in a low phosphorus, high nitrate condition; set E and F in a low salt condition.

Different media were used; tap water; a complete Hoagland solution (+ P 32); a solution with a reduced phosphate concentration (+ P 6,5); a solution without phosphate (— P) and a solution without nitrate (+ P 32, — N). All nutrient solutions were made with tap water.

same time however, nitrate was withheld (a combination of the treatments A and C). The growth and the uptake of this fourth set during the first period of the experiment was already rather different from the first three sets, particularly as there was a smaller number of young leaves appearing. This was the reason why A, B and C were used for the three main treatments. In spite of this drawback the results for this fourth set were quite clear. After supplying the phosphate, growth took place almost the same as it did with set C. From this it appears that this promotion of the growth was not the result of a renewed nitrate uptake. Nor could this be expected with this nitrate saturated material. If the set was then placed on a solution with nitrate but without phosphate an enormous uptake of nitrate took place, the rate was even higher than it was at the beginning of the experiments. Afterwards there was a slight fall, but the rate of uptake remained at a high level. This result once more points to the indirect influence of the phosphate supply on the absorption of nitrate.

The two low salt sets remained on tap water during the first period of 4 days. Then one set (fig. 9: E) was placed on a nutrient solution without phosphate. In spite of the fact that important ions were now being administered there was as with set A, a gradual fall in the growth. At the start of the experiment the low salt material was less strongly developed than were the high nitrate- low phosphate sets. This has to be ascribed to the lack of important ions like nitrogen and potassium. During the experiment however, in the first place phosphorus has a limiting influence on the development. By this it is possible to explain why results were obtained more easily in this way with high nitrate- low phosphate than with high phosphate- low nitrate material. The course of the nitrate uptake is also comparable with that of the high nitrate sets in that after some days the uptake comes to a standstill. In this respect these low salt plants can be compared with excised low salt root systems. As HOAGLAND and BROYER found (1936), low salt roots soon reach their maximum salt concentration. They ascribed the cessation of the absorption to the limited capacity of the roots for constructive metabolism associated with growth. This limited growth might be due to a deficiency of some elements e.g. nitrogen and phosphorus.

The second low salt set, which was placed on a complete Hoagland solution, also showed a rapid fall, but the uptake did not stop: after some time there was even a slight increase. This can only be the result of the growth, promoted by the phosphate supply.

Discussion

The results have already been amply discussed by the author (HELDER 1951). Hence a few remarks concerning the essentials will suffice.

In the first place it appeared that during the experiment the lack of phosphate especially depressed the development. By supplying phosphate this depression could be released. If a large quantity of phosphate was administered the vigorous growth continued, even when phosphate was once more withheld.

At the beginning of the experiment all sets still showed a vigorous nitrate uptake which however decreased rapidly and stopped if no phosphate was added. That this was due mainly to the as yet unsaturated condition of the material, appeared from the similar behaviour of low salt and high nitrate- low phosphate material. During the pretreatment the solutions of the last kind of material were renewed twice a week. Apparently this does not suffice to bring the material into a high nitrate condition, because for that it is necessary to renew the solutions diurnally, as was done during the experiment.

Phosphate being withheld, growth was inhibited more and more and the uptake of the nitrate came virtually to a standstill. This standstill of the uptake proved not to be the result of a direct influence of phosphate deficiency on an active absorption mechanism (compare DAVIES and OGSTON 1950), but of the saturated nitrate condition. If nitrate was not supplied for a few days, some nitrate could afterwards be taken up again as a result of the continued, though very slight growth. A real enhancement of the uptake was only found if phosphate was supplied, which removed the factor depressing the growth. It is a well-known fact that phosphorus is of great importance in the synthetic processes of the cytoplasm (NELSON 1946). The protein synthesis is especially depressed by a phosphorus deficiency. An accumulation of soluble nitrogen compounds and sugars is connected with this (WILLIAMS 1938; RICHARDS and TEMPLEMAN 1936; GREGORY 1937). Slightly different results were found at first by SCOTT EATON. Later however he obtained results which were more in agreement with current notions (SCOTT EATON 1949, 1950). So in the first instance the synthetic processes are stimulated by phosphorus supply, and nitrate ions are utilized. Strictly speaking these experiments showed that under certain conditions the utilization of nitrate ions can be a determining factor for the absorption. These synthetic processes however, are so intimately connected with the formation of protoplasm that it seems justified to speak of growth of protoplasm and to hold this responsible for the nitrate uptake. Increased formation of protoplasm as a result of the administering of phosphate leads to increased meristematic activity. (NELSON 1946; BURSTRÖM 1947). Further, this increased rate of cell division, leads after cell elongation to the promoted, outwardly perceptible growth. As far as roots are concerned, this means at first an enlarged absorbing surface. In the second place, as a result of cell elongation, a renewed accumulation in the vacuoles of root and shoot is made possible, by which an increased uptake is also made possible. Therefore a close relation between this growth, which depends on cell elongation and uptake which is mainly determined by protoplasmic formation cannot be expected. Under these circumstances it is a question of taste if one prefers to speak of the growth as a determining factor for the uptake, or not. Whenever this might give rise to any misunderstanding, utilization will be used instead of growth.

Meanwhile it will be clear why the results obtained concerning the nitrate absorption were more clear cut than those concerning growth, because the growth measured was mainly based on cell elongation and this need not stop immediately if protoplasmic growth has become very slight. Moreover, only the growth of the shoot was measured. Not is this only rather a crude index of the development but it is also a not very obvious measure of the quantitative significance of the root growth.

6. THE COURSE OF THE PHOSPHATE UPTAKE IN LIGHT AND DARKNESS

As was already stated in the introduction, the starting point of these experiments, was the continuation of ALBERDA's investigation (1948) into the influence of light and darkness on the course of phosphate uptake. In particular it was important to experiment with low salt plants, so that the results of both types of material (low salt and high salt) can be mutually compared.

In principle it now seems possible to interpret the results of these experiments with the aid of the points of view put forward in the preceding sections. Firstly, the sugar supply proved to be of primary significance to the phosphate uptake. Next in importance to the sugar supply is the salt condition. Taking into account these two conditions and the various processes being important to the uptake, an explanation was attempted of the course of the uptake in light and darkness. In order to judge the correctness of the explanations, material was harvested and analysed from different moments in the experiments. As will appear from the analytical results, variability was too large to render possible any decisive conclusion. In spite of this a possible explanation will occasionally be given with the description of the experiments. Of course, it must be stressed that these explanations are of a hypothetical nature.

Because the sugar supply is an important factor for the phosphate uptake, it need not surprise us that the light intensity used in these experiments has an influence on the results. As a matter of fact, the results obtained during the first year of experimenting (1948) when a moderate illumination was used, differed slightly from those obtained during the next year, when high light intensity was available. The experiments will be discussed in two corresponding groups.

a. *Experiments with moderate light intensity*

The experiments of 1948 were performed with an illumination of fluorescent lamps (fig. 1: A). Moreover, the plants were standing in the case used for the experiments concerning the influence of carbon dioxide-free air on the phosphate uptake. The case was not closed. But with the open case and this low light intensity, the development of the plants was less prosperous than during the next year, when the case was removed and a high light intensity was used.

In the first place the different behaviour of low salt and high salt material was studied. It appeared that there is only a relative difference between high salt and low salt material. Hence the influence of light and darkness on low salt plants was examined more closely. Solutions of various concentrations were used, allowing the low salt sets to change into a high salt condition variously rapidly.

Experiment 6a. To be able to compare low salt and high salt plants, three sets of plants of low salt as well as high salt were grown at the same time (June—July 1948). At the start of the experiment they were 6—7 weeks old; that is a little older than was the case for the bulk of the experiments. The plants were slightly taller, and as a result of this they were hindered more by the limited space of the case. The solutions were renewed every twelve hours and the uptake was

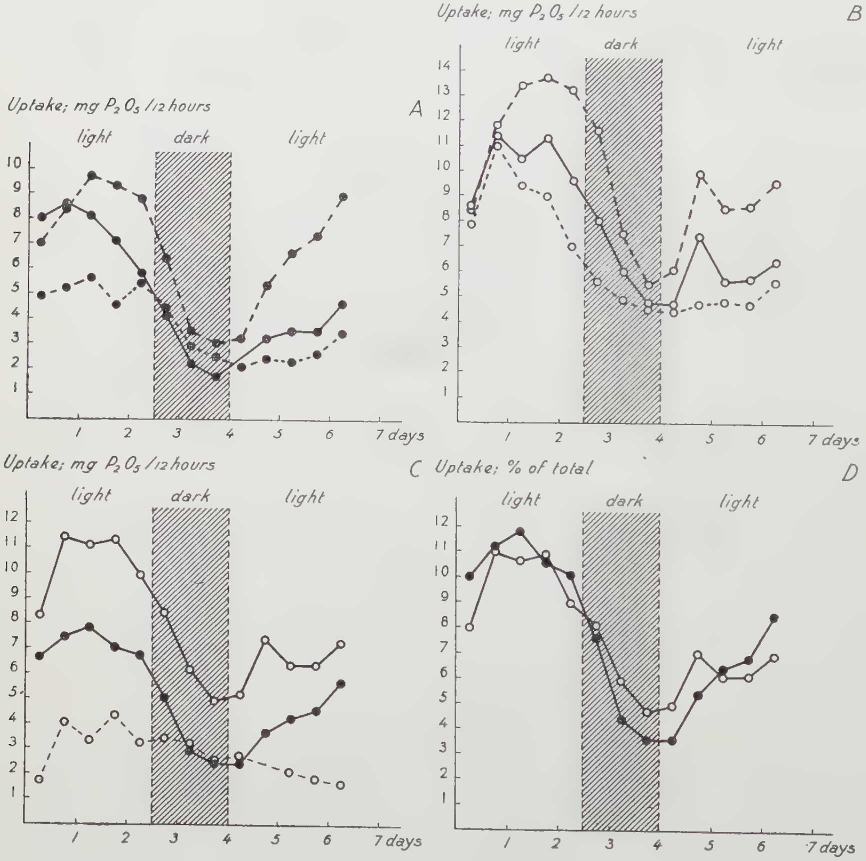


Fig. 10. The course of the phosphate uptake in light and darkness. A: three sets of high salt plants. B: three sets of low salt plants. C: Mean value of the rates of uptake of the high salt and low salt sets and their difference (a crude index of the accumulation in the vacuoles of the low salt plants). D: The mean amounts of phosphate, taken up by the low salt and high salt sets, expressed in percentages of the total amount, taken up during the course of the experiment.

determined. A half-strength Hoagland solution was used. Fig. 10 shows the course of the uptake.

The course as a whole was the same for all sets (fig. 10: A and B). Initially there was an increase in the uptake in the light followed by a slight decrease. During the dark period the uptake fell rapidly. This fall decreased at the end of the dark period and changed into an increase during the second light period. It appears from the mean values of the high salt and low salt sets, that the uptake by the low salt plants was greatest (fig. 10: C). The initial increase was also clearest with this material. Both types of plants showed a large variability as to the uptake values. As a resuls of this the high salt set with the largest uptake is comparable with the low salt sets with the lowest uptake.

Experiment 6b. In this experiment low salt plants were exclusively used. Eight sets were grown during July and August 1948. They were six weeks old when used in the experiment. As a result of the favourable circumstances they were in excellent condition. Uptake rates were determined on Hoagland solutions of four different concentrations (12·5, 25·0, 37·5 and 50 %). At each concentration two sets were used. The course of the uptake is represented by fig. 11. The mean values of the two sets at each concentration is indicated.

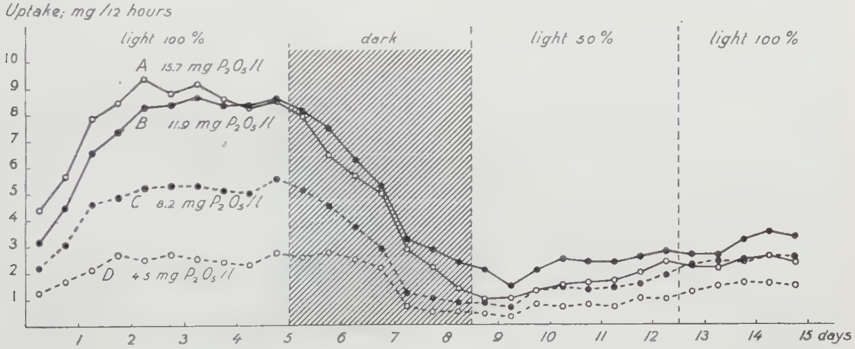


Fig. 11. The course of the phosphate uptake by low salt plants in light and darkness at different external phosphate concentrations.

The influence of the concentration is clear. The higher the concentration, the higher was the rate of uptake. The uptake also increased in this experiment. A constant level having been reached, the absorption rates were at increasing concentrations: 2·5, 5·3, 8·5 and 8·8 mg P_2O_5/12h. With the two sets at the highest concentration there was a small but definite decline in the uptake. But with the other sets a decline of the uptake, as occurred in the previous experiment, was out of the question. During the dark period the uptake of all sets, except for those standing on the lowest concentration, immediately decreased. With group A and B, this decline was larger than that with group C. With the fourth group the uptake continued at the same rate for some days, but afterwards it also declined. At the end of the dark period all sets showed only a small uptake. Group B now absorbed rather more than group A.

If after this, the plants were again placed in light, the uptake rose only slowly after some retardation. This was due to the very low light intensity; two instead of four lamps being used. After four days the other two lamps were also switched on, but no clear influence could be observed. The uptake of group B remained the largest one, while the difference between A and C had disappeared.

Discussion

In order to explain the course of the uptake of the high salt plants it is obvious to think of the sugar supply, in view of its significance for the phosphate uptake. Besides, high salt roots are known to be in a low sugar condition. Hence, the cessation of photosynthesis in darkness may be expected to cause a fall of the phosphate absorption in a short time. For as much as the uptake depends on the consumption, the fixation by growth may be expected to be of primary importance. This growth is closely connected with the sugar supply. That is why it is dependent on the illumination. But it is conceivable that there are other effects of light on the growth and uptake.

The average uptake by low salt plants was larger than the uptake by high salt plants (fig. 10: C). Moreover, there was a marked increase at the beginning of the experiment. This must depend on the fact that the various processes, by which the rate of uptake is determined, had to be put into motion, because during the pretreatment, the whole absorption process was stopped. That this went on so slowly, doubtless depended on the low salt condition. As far as the uptake was determined also in this case by growth, this conclusion is obvious. From the previous section, growth appeared to be mainly depressed by phosphorus deficiency. Phosphorus supply enhanced growth and by this enhanced the nitrate absorption. The same can be expected with respect to the phosphate uptake. The enhanced phosphate uptake in its turn, will again promote growth. In this way a mutual promotion of growth and phosphate uptake could occur during the first days of the experiment.

At first sight the further course of the uptake by the low salt plants was of the same nature as it was with high salt plants. It is true that the fall in darkness was steeper and the rise in the light afterwards was smaller, so that there was less difference at the end of the experiment than there was at the start. Such solely quantitative differences also existed between the sets of one type of material. On closer examination however it appears that there are indeed vital differences.

This difference is demonstrated by comparing the average uptake rates of the high salt and low salt sets, if the absolute difference in uptake rates is neglected. For that purpose the average amounts of phosphate taken up during the twelve hours period, are expressed as percentages of the mean total amounts of phosphate, taken up by the two types of material. These percentages are plotted in figure 10: D.

It shows that the uptake by the high salt plants decreased in darkness and increased during the second period more intensively than did the uptake by low salt plants. Thus, the high salt plants were more sensitive to the alteration of light and darkness than were the low salt plants. As far as the decrease in darkness is concerned, this might be connected with the greater sugar storage of the low salt material. But, if this is so then it is difficult to see why afterwards, the increase in the uptake by low salt plants in light is so small. Rather, the different sensitivity points to a difference in the nature of the uptake in these two types of material. It is obvious to surmise that this is determined by the salt condition, as a result of which the uptake by the high salt plants is compounded in another way than is the uptake by the low salt plants. While uptake by high salt plants is largely dependent on the growth and accumulation in the vacuoles is of minor importance; with low salt plants, the accumulation in the vacuoles is also of importance. Both processes may depend on the illumination to a different extent. For with low salt plants sugar has been accumulated in the vacuoles giving at the same time an osmoregulation (HOAGLAND and BROYER 1936). Such an osmoregulating principle was also met with by DELEANO und ANDREESCO (1932) in leaves of *Salix*. They observed a loss of salts in senescent leaves. At the same time the concentration of monosaccharides was enlarged and thus, the osmotic concentration was kept at a fixed level. These data point to an intimate connection between ion accumulation in the vacuoles and the sugar stored in the vacuoles. If this assumption is correct, it may easily be seen why the accumulation with the low salt plants (and hence the total uptake by these plants) is far less sensitive to an alteration of light and darkness than it is with high salt plants.

To obtain an impression of the rate and the course of this accumulation in the vacuoles by the low salt plants, the difference between the absorption rates of low and high salt material might tentatively be taken. It should be realised that the uptake by the high salt plants was not solely based on the fixation by the growth. On the other hand, the growth of the low salt plants was not so vigorous as that of the high salt plants, at least not at the commencement of the experiment, owing to the unfavourable pretreatment. Hence, the accumulation rate of the low salt plants will certainly have been larger than the difference between the uptake of low salt and high salt plants. This difference, shown by fig. 10: C, must therefore be considered as a rough approximation.

As the figure shows, the accumulation in the vacuoles increased just a little at the start. It is difficult to judge the significance of this increase. Perhaps the true value of this increase was lower. Further, the rate remained at about a constant level during three days and then decreased gradually. There was not the slightest sign of any influence of light and darkness, so that the conclusion, low salt plants are less sensitive to light and darkness because their uptake is to a large extent due to the accumulation in the vacuoles, seems justified.

The diminishing of the difference in the uptake of low salt and high salt plants indicates that the low salt sets came gradually into a high salt condition. On the grounds of the considerations just mentioned it could be expected that the smaller the change into a high salt condition, the smaller the sensitivity to a dark treatment. This was completely confirmed by the results of the second experiment. The higher the concentration of the solution that the plants were placed on, the higher the rate of uptake, and as a result of this the higher the velocity with which the plants attained a high salt condition. The effect on the course of uptake was in accordance with this, as is shown by fig. 11.

b. Experiments with high light intensity

With the experiments of 1949 incandescent lamps were used as a light source (fig. 1: B). As appeared from some of the experiments, under these conditions sugar supply to the roots was not a limiting factor, since the addition of glucose to the nutrient solution had no effect on the phosphate uptake (exp. 3*c*, *d*; 4*b*). The case that was used in the experiments concerning the influence of carbon dioxide-free air was removed, so that there was no danger during these experiments, which were prolonged for many days, that the growth of the plants was impeded. Moreover, it was now possible to measure the growth of the shoots and in this way to obtain an impression of the rate of the growth processes. The sets consisted of twelve plants and the measurements were made every twelve hours and hence very regular results could be obtained with these experiments.

In order to gain a further insight into the various factors influencing the uptake of high salt and low salt plants in light and darkness, some sets were harvested during these experiments and the phosphate contents determined.

Experiment 6c. The six sets of plants in this experiment were grown during the months May and June 1949. Conditions were not yet optimal. The plants were only small and this partly explains the low rate of uptake (fig. 12: B). During the first 2—3 days the uptake increased, it then continued at a constant rate. In darkness the uptake fell immediately, but soon attained a new constant level, which was nearly equal to the rate of uptake at the start of the experiment. This suggested that the uptake in light was a result of the promotion of growth. The course of the growth agreed with this. It increased during the first days, attained a constant level, fell in darkness and came virtually to a standstill. This development of the growth depends mainly on cell elongation which can continue even if the protoplasmic formation is stopped. Hence, the utilization of phosphate by the growth processes in these experiments will be stopped before the visible development comes to a standstill and also by this the absorption, as far as it was determined by this utilization.

At the end of the light period and of the sixth and seventh day, two sets were killed and analysed. If growth is checked in darkness, but uptake goes on at a reasonable rate, the phosphate content can be expected to increase. As appears from table IV, the results are too variable to make it possible to conclude if this applies to this experiment.

Experiment 6d. The seven sets of this experiment were grown during the favourable summer months July and August 1949. The plants were more vigorous than those of the last experiment and the uptake was much larger. The light period lasted only two days, so the duration of the dark period could be extended to six days.

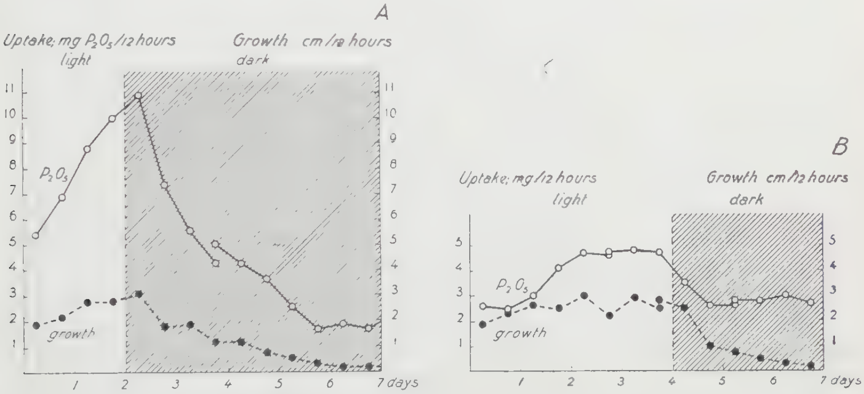


Fig. 12. The course of the phosphate uptake by low salt plants and the growth of their shoots in light (high intensity) and darkness. A: Sets of plants grown in midsummer. B: Sets of plants grown early in summer. The breaks of the curves are due to the removal of sets of plants.

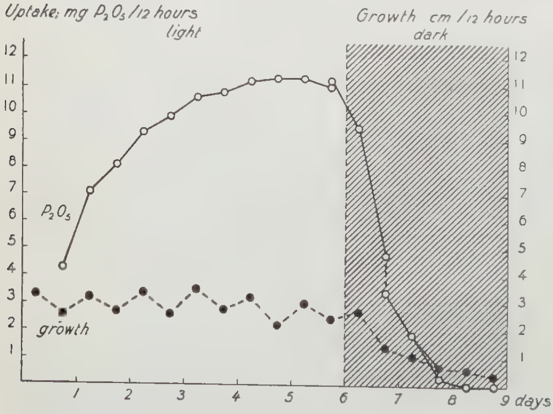
As is shown by fig. 12: A, the uptake at once rose rapidly. The plants being placed in darkness this increase continued for some time and then the uptake diminished very gradually. After four days of darkness it had not yet stopped. On the contrary, it afterwards showed a constant, though low velocity. On the last day of the experiment the phosphate determinations were a little irregular; they have been omitted from the figure. The shoot development runs completely parallel to the uptake. The decrease in darkness was likewise very gradual. This decrease, however, continued until it at last became zero. The synthetic processes will be stopped earlier. Perhaps the breaking off in the decrease of the uptake on the sixth day was connected with this.

Two sets of plants were harvested at the end of the second, the fourth and the eighth day. There was an increment of the phosphate content in darkness (table IV). After the fourth day no significant alteration could be observed. The uptake by the sixth set was much lower than that by the other sets. The shoots of this set were excised on the second day. The uptake by the remaining root system fell rapidly at first, afterwards it rose again and though the course was irregular, the rate of the uptake at the end of the dark period was larger than that of the intact plants. Such an enhanced absorption rate by an excised root system was also observed in experiment *3d* (fig. 4). The correct explanation of this result is hard to give for the moment. At any rate it points to some interaction of shoot and root, important to the uptake.

Experiment 6e. High salt plants were used, grown during June 1949. There was a prosperous development. The most striking result of this experiment was the enormous increase in the uptake during the light period (fig. 13). Only after four days was a constant level attained. This behaviour, so different from that found with low light intensity can only be explained by the use of the high light intensity, and the large sugar production connected with it. This sugar production can enhance the accumulation in the vacuoles and the fixation of phosphorus by growth. However, neither of these two processes seems to give a sufficient explanation of the enormous increase of the uptake in light. Another possibility is an enhanced consumption by the formation of hexose phosphate. This hypothesis is very tempting in this case, for it can explain at the same time the rapid fall of the uptake in darkness. During the continued sugar consumption in darkness, bound phosphate will be liberated. As a result of this the uptake of inorganic phosphorus from the medium will be depressed and may even be stopped before the growth processes have come to a standstill.

The rhythm of the growth could be observed extremely well. This rhythm also occurred in the other experiments, though less clearly. The largest growth took place during the night in spite of the continuous illumination. The basis of this rhythm remains uncertain. It may be based on the cell divisions as well as on the cell elongations.

Analytical data were obtained at the beginning of the experiment,



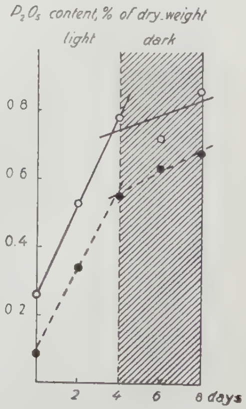


Fig. 13. The course of the phosphate uptake by high salt plants and the growth of their shoots in light (high intensity) and darkness. The breaks of the curves are due to the removal of sets of plants.

Fig. 14. The course of the phosphorus content of shoots and roots of low salt plants if they are allowed to take up phosphate from nutrient solutions, that are renewed twice a day.

at the end of the light period that lasted for six days, and after the first, second and third day in darkness. There was no sign of any alteration in the phosphorus content. But an obvious increment of fresh- and dry weight did occur. It was based mainly on the large growth of the shoots.

Experiment 6f. In order to obtain comparable data of low salt and high salt material five sets of each type were grown at the same time (June—July 1949). The sets were placed in the light during four days, and afterwards in darkness for four days. A high salt set and a low salt set were harvested at the start of the experiment and then every other day. When choosing the sets for analysis, some selection was applied in such a way that the sets at the start and at the end of the light and dark period were as equal as possible to look at. Thus the other sets, harvested at the fourth and sixth day, varied a little in development of the roots or shoots.

As a result of a failure of the photelometer the absorption values could not be determined exactly. For the sake of the analytical results the experiment was continued. Both kinds of material showed a large increase in the uptake during the first days. Only at the fourth day was a constant level attained. Afterwards, in darkness the uptake decreased gradually with both kinds of material by about the same extent. During the whole experiment the uptake by the high salt plants was larger than that of the low salt ones. This was a result of the low salt plants being less well developed owing to the salt deficiency.

The growth increased during the first days, then it remained at a constant level and diminished in darkness very slowly. During the light period all sets showed the day and night rhythm. The growth of the high salt plants was a little stronger than that of the low salt ones, throughout the experiment. The total picture looked very much like that obtained with the low salt plants of experiment 6*d*. (fig. 12: A). This involved that the high salt plants showed a behaviour differing from that during the last experiment. This may be connected with the conditions during the pretreatment. The growth was more rapid than with the high salt sets of the previous experiment, grown early in summer. This implied at the same time, that the plants did not attain an extremely high salt condition. This is also shown by the analytical results (table IV). On the other hand there was a good illumination allowing a sufficient sugar supply. It is not surprising that, owing to these various factors, the behaviour of the high salt plants was much like that of the low salt plants.

Discussion

A summarizing picture of the course of the uptake of low salt and high salt plants in light and darkness will be given in the general discussion. This discussion will be restricted to a few supplementary remarks concerning the analytical data. As had appeared in the description of the experiments, the value of the analytical results

TABLE IV

The fresh weight, dry weight, phosphorus content, total amount of phosphorus, and shoot- root ratio of the sets of plants, harvested at different moments in the experiments concerning the influence of light and darkness on the uptake of phosphate

Material	days	Shoot				Root				Shoot-root ratio	
		fresh weight g	dry weight g	P_2O_5 content %	total P_2O_5 mg	fresh weight g	dry weight g	P_2O_5 content %	total P_2O_5 g	fresh w.	dry w.
Low salt . . . . . Exp. 6*c*; fig. 12B	4	44.8	4.00	0.77	30.8	36.0	2.66	0.89	23.7	1.2	1.5
		41.0	3.55	0.50	17.8	35.0	2.21	0.68	15.0	1.2	1.6
	6	60.0	5.16	0.67	34.6	47.3	2.84	1.02	29.0	1.2	1.8
		44.5	3.85	0.63	24.3	37.0	2.43	0.68	16.5	1.2	1.6
	7	59.0	4.83	0.80	38.6	47.0	2.69	1.08	29.1	1.3	1.8
		66.5	5.66	0.63	35.7	50.3	2.88	0.91	26.2	1.3	2.0
Low salt . . . . . Exp. 6*d*; fig. 12A	2	77.0	8.14	0.47	38.3	50.5	3.24	0.52	16.8	1.5	2.5
		86.0	9.47	0.26	24.6	—	—	—	—	—	—
	4	75.0	7.36	0.65	48.6	42.0	2.63	0.65	17.1	1.8	2.8
		89.0	8.77	0.60	52.6	43.0	2.50	0.65	16.3	2.1	3.5
	8	—	9.19	0.60	55.1	—	2.78	0.82	22.8	—	3.3
		—	7.94	0.75	59.6	—	2.76	0.90	24.8	—	2.9
High salt . . . . Exp. 6*e*; fig. 13	0	33.0	3.55	1.50	53.3	21.5	1.80	1.26	22.7	1.5	2.0
	6	142.0	9.38	1.43	134.1	51.5	2.80	1.34	37.5	2.8	3.4
	7	236.0	17.17	1.04	178.6	78.0	4.40	1.13	49.7	3.0	3.9
	8	134.0	9.12	1.37	124.9	45.0	2.38	1.42	33.8	3.0	3.8
	9	206.0	13.34	1.08	144.1	64.0	3.19	1.33	42.4	3.2	4.2
High salt . . . . Exp. 6*f*.	0	154.0	14.28	0.80	114.2	60.0	3.91	0.88	34.4	2.6	3.7
	2	205.0	21.12	0.67	141.5	77.5	4.43	0.68	30.1	2.7	4.8
	4	216.0	21.30	0.73	155.5	62.5	2.90	1.02	29.6	3.4	7.3
	6	—	—	0.76	—	—	4.34	1.11	48.2	—	—
	8	150.0	12.90	1.17	150.9	58.0	2.50	1.62	40.5	2.6	5.2
Low salt . . . . . Exp. 6*f*.	0	58.0	8.03	0.09	7.2	63.0	3.90	0.26	10.1	0.9	2.1
	2	69.5	7.81	0.28	21.9	46.0	3.02	0.49	16.2	1.5	2.6
	4	73.0	7.24	0.51	36.9	45.0	2.57	0.67	26.1	1.6	2.8
	6	—	7.85	0.59	46.3	—	3.24	0.79	24.4	—	2.4
	8	59.0	6.69	0.59	39.5	48.5	—	1.05	—	1.2	—

(table IV) is highly reduced by the large variability. This applies mainly to the fresh- and dry weight figures and hence to the absolute amounts of phosphate. Therefore only large differences find expression.

The fresh weight of the roots of the low salt plants was nearly the same as that of the shoots. With the high salt plants the fresh weight of the shoots was 2—3 times that of the roots. It is clear that the development of the shoots was highly depressed by the low salt treatment. The total amount of phosphate present in the low salt shoots equalled the amount present in the roots. With the high salt plants the ratio was also two or three. This means that during the pretreatment at least 2—3 times as much phosphorus was transferred to the shoots as was stored in the roots themselves. With a low salt treatment half of the phosphate absorbed was fixed in the root (Williams 1948). During the experiments the low salt plants were able to absorb large quantities of phosphate. In experiment 6*f* more than twice the amount that was accumulated in the roots themselves, was transferred to the shoots. In experiment 6*d* the ratio was even more favourable, as the shoots were relatively larger.

The most regular results are given in the figures of the phosphorus content. The values are expressed in percentages of total dry weight. The drawback however is, that alterations in phosphorus content may delude us. They may be the result of alterations in dry weight e.g. by the consumption or production of sugar. This disturbing factor will be taken into account as much as possible.

With high salt plants, no clear alterations in the phosphorus content could be observed. In experiment 6*f* the percentage appeared to increase in the darkness. This may be the result of a continued uptake and a simultaneous inhibition of the growth, so that the plants became saturated. This is in accordance with the course of uptake observed, which bore a close resemblance to that of the low salt plants. This pointed to their not being very high salt. Indeed, the phosphorus content was not as high as it was with the plants of experiment 6*e*. It is striking that the percentage rose mostly in the roots. With experiment 6*e* the plants were in an extremely high salt condition. No change of the phosphorus content occurred, nor could this be expected with material in which uptake was mainly determined by growth.

The low salt sets gave more obvious results. In spite of the large variability a rise in the phosphorus content could be observed during the first days of the experiment. This was due to the low content at the commencement of the experiment. In fig. 14 the data of various experiments have been summarized (fig. 12: A and B; exp. 6*f*). In two experiments the light period lasted for four days, in one experiment for only two days. In spite of this the data agrees rather well. There was an increase in the content during the first four days. Afterwards the increase was only slight and may be the result of the sugar consumption. This result supports the supposition that the uptake by low salt plants is to a large extent independent of the illumination and is determined by the salt and sugar condition (osmoregulation). The level finally attained almost coincided with that of the high salt plants of experiment 6*f* (0·69 resp. 0·76 %). This means that the plants though they did not develop to an extremely high salt condition, attained a reasonable salt level. With this material also, the phosphorus content of the roots was higher than that of the shoots.

The gradual diminishing of the differences between high salt and low salt plants also appeared from the course of the shoot-root ratio. The ratio values were variable. Two conclusions may be drawn. In the first place this ratio increased obviously with low salt plants during the experiments. This was connected with the very low value at the beginning of the experiments. In the second place, in spite of this increase, the favourable ratio of the high salt plants was not attained. The average value of this ratio with low salt plants after the fourth day of the experiments was: 1·4; with high salt plants: 2·8 (on dry weight basis: 2·4 resp. 4·1). Thus the ratio for high salt plants was twice that for the low salt ones. As far as the demand for salts is different between shoots and roots, this difference in shoot-root ratio must have had an influence on the uptake. The sensitivity to light is also very likely to be larger with plants with relatively large shoots. However, the large agreement in the course of uptake and growth between the high salt material and the low salt one of experiment 6*f* indicates that the salt condition is more significant than the shoot-root ratio.

IV. GENERAL DISCUSSION

Permeability, physico-chemical and biochemical principles

The first stage of the uptake by intact plants consists of an entering of the anions into the cytoplasm of the cells of the epidermis and perhaps into the cortical cells of the roots. Whether the anions can permeate into the cytoplasm easily is of primary importance. Therefore this problem needs to be discussed first.

In the experiments on the loss of salts it was found that amounts, comparable with those of the uptake, can be readily given off. This was conceived as an indication, that phosphate can permeate easily into and out of the cytoplasm of the root. The permeation was considered a passive process, in which special forms such as accelerated diffusion may play a part.

Meanwhile, Steinbach (1951) pointed out that this concept is an oversimplified one in the light of recent investigations. It is possible that ions are bound in the cell membrane to a specific substance. Then the complex is decomposed and the ion is liberated into the cytoplasm. On ground of analytical data for medium and cytoplasm in such a case the interference might be drawn erroneously, that there is an easy passive permeation. That which applies to the penetration of ions seems also to be applicable to their loss. Thus, Gale (1947) found that the loss of free lysine with *Streptococcus faecalis* depends on metabolism. A large loss of phosphate was obtained with *Chlorella* *pyrenoidosa* and *Rhodospirillum rubrum* by KAMEN and SPIEGELMANN (1948). They could demonstrate that the leakage occurred mainly at the expense of the fraction extractable by trichloracetic acid. In this connection they point to the difficulty in determining the exact inorganic phosphorus content. They showed that by trichloracetic acid instable phosphorus compounds were broken down and extracted. This is important for the interpretation of the data. As KAMEN and SPIEGELMANN expounded, it seems that a choice must be made between two possibilities. Firstly it may be that the ion diffuses into the cell and is afterwards metabolised. Secondly, there may be some esterification on the surface of the cell followed by a breakdown as a result of which the ion is liberated into the cytoplasm. The experiments on the significance of the sugar supply and the preliminary results of the experiments on the phloridzin inhibition pointed to the second possibility. Moreover, discussing the results of the experiments over the relation of uptake and concentration, this second possibility proved to be a valuable hypothesis in the explanation of the "adsorptive" relation. It involved that the substance, to which phosphate is bound in first instance, is supposed to be present in a small amount. As a result of this the first stage may be the determining factor of the rate of the absorption process. STEINBACH also points to this possibility.

Meanwhile the two principles do not exclude one another. The possibility remains that ions also enter in a more physical way. This diffusion is generally assumed to be slow. This may be due to some outer membrane of specialized structure. It may also be the result of the presence of large indiffusible anions in the cytoplasm (ROBERTSON 1951; FREY-WYSSLING 1948). If the former is correct, the esterification process is necessary to transfer the anions through that outer membrane. It must be also localized in that membrane. Indeed this is generally accepted. This idea is supported by investigations e.g. those of Rothstein and collaborators (ROTHSTEIN and MEIER 1948), which showed that a lot of enzymes important for sugar metabolism are situated in the surface of yeast cells. Rothstein and Meier emphasize that the results need not mean a surface in a strict mathematical, two-dimensional sense.

However, if the resistance is supposed to be situated in the whole cytoplasm, the necessity to localize the active process in the surface, vanishes. Admittedly there may be some differentiation of the cytoplasm for this process. The phosphorylation processes, being so intimately connected to sugar metabolism, can be expected mainly to occur there, where the latter is dominant. With plant cells this applies (for example) to the outer layer of the protoplasm, that is engaged in cell wall formation (STREET and LOWE 1950). This also does not mean a localisation in a surface layer of molecular dimensions for, it is clearly shown by electronic microscopic pictures of young cell walls, that the cellulose elements are not only formed by the external membrane but by an outer layer of the cytoplasm of measurable thickness. The whole young cell wall is so to speak, soaked in protoplasm (Frey-Wyssling, Mühlethaler und Wyckoff 1948; Mühlethaler 1950; Roelofsen and Houwink 1951). Phosphorylations are also coupled with the cyclophorase system that is to a large extent situated in the mitochondria.

One arrives at the conclusion that, if some esterification of phosphate is an essential condition for its uptake, this need not entail that the process goes on exclusively at the surface of the roots. Diffusion in its different aspects may play an additional part. Some differentiation between an outer and an inner layer of the cytoplasm seems likely. No doubt, uptake due only to diffusion processes is of minor importance. Change in the composition of the medium will cause the establishment of new Donnan equilibria. Initially some uptake or loss may occur as a result of this, as was found in the experiments on the loss of anions. In these experiments the plants were in a condition of low metabolic activity, large changes in the external concentrations being applied at the same time.

If these conclusions are correct, it means at the same time that a sharp distinction between entrance into the cytoplasm and a further transport in the cytoplasm or symplasm of the root cannot be made. The same principles may hold good for both. An important question remains viz. by what factor the direction of transport is determined.

The significance of metabolism, especially the significance of respiration to the anion uptake has been shown for years by Lundegårdh. The cytochrome-cytochrome oxydase system has been held responsible for the uptake in his well-known concept of the mechanism of anion transport. Small supplements have been added by Burström (1951). Robertson and his collaborators (Weeks and Robertson 1950) have attained results that support the principles of Lundegårdh's theory to a large extent. That the theory is not yet generally accepted in spite of this, might be ascribed to the following circumstances.

In the first place the cytochrome system take a central position in the whole of the energy supplying processes. Hence it is not surprising that the inhibition of this part of the respiration impeded the energy consuming process of anion absorption. A more complicated connection between uptake and respiration seems more likely (Hoagland 1948). This concept is supported by the data, that indicate the significance of phosphorylations (Nance 1949; Robertson, Wilkins and Weeks 1951). It should however be admitted, that on the one hand, the quantitative relation between oxygen consumption and anion uptake is in good accordance with that which can be expected on grounds of Lundegårdh's view. On the other hand the effect of the phosphorylation might be due to their influence on the maintenance of enzymatic structures important for the ion uptake which are present in mitochondria (Green 1951). That in spite of this the relation of cytochrome and uptake is finally more indirect in its nature seems to be confirmed by the fact that anion uptake also occurs with cells and tissues which are lacking cytochromes. So

Österlind found with *Scenedesmus quadricauda* that the respiration was not inhibited by cyanide, but the anion uptake was (Österlind 1951).

A second point significant to the judgement of the cytochrome mechanism, is the specificity of the uptake. Ions are known to be absorbed in quantities, the ratio of which is quite different from that of the composition of the external solution. Moreover, the uptake of an anion proved to be independent of the uptake of other kinds of anions (Arisz 1945; Alberda 1948; Humphries 1951). This could be affirmed by some experiments of the author not mentioned here: the uptake of phosphate was not affected by the presence or absence of other ions. Of course, secondary effects may occur. This was clearly demonstrated by the experiments on the influence of the utilization on the uptake of nitrate by phosphorus deficient plants.

This independent behaviour of the uptake of various anions can with difficulty be squared with the unspecific cytochrome mechanism. It requires at least some supplementary mechanism, that is adjusted to the nature of the anion. This might consist of binding it to some carrier. This formation may be connected with metabolism (Steinbach 1951) so that the cytochrome system may be concerned with it. Afterwards, the anion, once it has entered into the cytoplasm, might be transported by the cytochrome system as it is assumed to be. The question whether this applies, is closely connected with the question as to the form in which phosphate is transported. Arisz (1952) indicated the resemblance in the transport of organic substances like amino acids and inorganic ions. In particular, with regard to phosphate it seems very likely, that to a larger extent it is transported in a bound rather than in a free state. Thus, phosphate transport may be compared with that of organic substances. The same principles: mass flow, diffusion, protoplasmic streaming may be valid.

The problem remains concerning the polarity of the transport. Lundegårdh assumed two factors. In the first place the direction might be determined by an oxygen gradient. He does not deem it to be an important factor, because large variations in the oxygen percentage of the medium are possible without any effect on the uptake. Then the direction must be due to some polarity of the structure of the cytochrome system. Thus the localisation of this cytochrome system is important. During the last years this system has proved to be bound to the mitochondria (Green 1951; Millerd e.a. 1951). It is difficult to say how the polarity of an uptake, that is connected with this system, given its localisation, can be explained.

In the opinion of the author such a polarity of the transporting mechanism is not a necessary requirement. There is a continuous consumption of ions, as they are fixed by synthetic processes, and secreted into the vacuoles and vessels of the root. What is required is some mechanism that levels concentration gradients in the symplasm of the roots. This might be a cytochrome mechanism or the protoplasmic streaming (also sensitive to HCN) by which ions, bound to protoplasmic particles (Arisz 1945) or mitochondria (Robertson 1950) or not, are transported in every direction. Such an undirected transport also explains the loss of ions if the utilization of the plants stops and dissimilatory processes become dominant.

Some remarks should be made concerning the possible role of the epidermis and cortex. According to BURSTRÖM the oxydative stage of the uptake would be situated in the epidermis. This concept is supported by the experiments of SANDSTRÖM (1950), who treated the roots with di-amylic acetic acid by which the cells of the epidermis are ruptured. The uptake by plants in which the epidermis has been peeled off in this way looks like a passive absorption of the ions owing to the transpiration stream. Particularly, the specificity of the anion uptake disappears. BROYER and HOAGLAND (1943) found that damage to the roots also results in a more passive uptake. Further examination of the effects of di-amyl acetic acid is desirable.

As distinct to this concept of BURSTRÖM many investigators assume the cortex as a whole to be in direct contact with the medium. This may be due to a great passive permeability or to the transpiration stream by which the ions can be transported passively at least through the cell walls of the cortex.

Summarizing it can be stated that biochemical factors are decisive as to the phosphate uptake. In view of the fact that inorganic phosphate is bound very rapidly (gel-P; Green 1951) this is not surprising. This renders it at the same time somewhat uncertain as to whether the mechanism of the phosphate uptake may be used as a model for the uptake of other anions (STEINBACH 1951). During the investigations discussed here, the need was felt more and more for studying also the uptake of another anion, that is linked up with metabolism to a lower extent. Unfortunately, the maize plant used, proved to absorb only a very small amount of chloride if any at all. However, the more significant metabolism is for the uptake of anions, the more it will be necessary to take into account the specific features of the anion in question. It is surely possible that the quantitative significance of the various absorption and transport principles depends on the nature of the anion.

PHYSIOLOGICAL FACTORS

The factors determinative for the uptake by the roots have been mentioned previously: the accumulation in the vacuoles, the secretion into the vessels, the fixation by synthetic processes (growth) and the supply of salts from the shoot.

The fact that the concentrations in the vacuoles of algae may be many times that of the external solution, was the starting point of the modern research into the salt accumulation. Afterwards the close connection between the absorption of ions and metabolism particularly with excised root systems and slices of storage tissue was stressed (STEWARD 1935; HOAGLAND and BROYER 1936; HOAGLAND 1948). Generally no sharp distinction was made between the absorption from the medium and the accumulation in the vacuoles. The active absorption mechanism was thought to be situated in the surface of the absorbing cells. Such a distinction between the uptake of anions into the cytoplasm and their secretion from the cytoplasm into the vacuole was made by ARISZ in 1948. With *Vallisneria* leaves he observed an accumulation of ions in the vacuoles in light. In darkness there was no uptake. If a part of the leaf, though not being in contact with the medium was illuminated, it showed accumulation in the vacuoles. The non-illuminated part of the leaf that was in contact with the medium had to absorb the substances. Then they were translocated to the illuminated part and there they were secreted into the vacuoles (vacuole-secretion theory: Arisz 1948). Thus we are fully justified in using the term vacuole-secretion, by which the similarity with the secretion to the vessels is stressed. In agreement with the usual terminology, accumulation has been used throughout this article. To avoid misunderstanding distinction has been made between total absorption and this accumulation in the vacuoles.

The significance of the accumulation in the vacuoles for the total absorption depends on the salt condition. With low salt plants it is to a large extent determinative in fixing the rate of absorption. As a rule the uptake by low salt plants will be larger than that of the high salt ones. On the other hand, owing to the low salt treatment the development of the plants is checked, mainly by the phosphorus deficiency. By this, in spite of the low salt condition, the rate of uptake may be lower than that of the high salt plants. The different composition of the uptake appears from the behaviour in darkness. The uptake by the low salt plants is less sensitive to a dark treatment. The accumulation in the vacuoles even continues undisturbed. But this accumulation decreases gradually during the course of the experiment as the material is attaining a higher salt condition. Along with this, the sensitivity of the total uptake increases. Low salt plants have a large amount of available sugar in their roots (HOAGLAND and BROYER 1936; ALBERDA 1948). It appears that this sugar is mainly of benefit to the accumulation. The result is that sugar is replaced by salt just as during the pretreatment sugar was stored instead of salt. This results in some sort of osmoregulation.

Another process by which the uptake is determined is the fixation of ions by synthetic processes. That the uptake can be enhanced or limited by growth seems very obvious on a priori grounds. But, if it is true, that even the very first stage of the uptake is connected with metabolism, such a direct regulating influence of the growth is far from being self-evident. Both processes, uptake and growth, may be based on the same metabolic conditions. A direct causal analysis is necessary, as was made in these experiments concerning the nitrate absorption. Nitrate utilization was inhibited by phosphorus deficiency, allowing a regulation of growth by phosphate supply.

The extent to which uptake is determined by growth processes, depends on a number of factors. Large differences may be found between nitrate, phosphate, sulphate and chloride as they are utilized by the plant to a different degree. Secondly, the external concentration is significant. With low concentrations the first stage of the absorption process may be limiting. This was observed in the experiments on the relation of uptake and external concentration. This process may also be limiting at higher concentrations viz. if the substance to which the anion is assumed to be bound, is present to a limited amount. If this does not apply, the utilization by the plants may impede a further increase in the uptake for rising external concentrations. This effect occurs only occasionally with low salt plants. On the other hand, with high salt plants it was obligatory. This is intelligible since the salt condition of the latter implies that the total consumption is mainly due to growth. As appeared from the experiments on the influence of light and darkness and on the effect of carbon dioxide-free air on the uptake, this growth, and through this the uptake, is sensitive to the sugar supply.

As well as being influenced by the salt and sugar condition of the plants, growth is influenced by a number of other factors, that may be partly hormonic in nature. The result is, that the growth of the root, and hence the uptake as far as it is influenced by this growth, also becomes dependent on factors and processes of medium and shoot.

The most specific activity of the root consists of the secretion of salts into the xylem vessels. With a reasonable salt supply the amount translocated to the shoot can be the larger part of the uptake, as is proved by considerable data concerning the salt content of roots and shoots. It could be deduced from the data of the plants used in these experiments, that with low salt material, equal amounts were present in the shoots and the roots; with high salt material the amount transferred to the shoots was 2—3 times the amount stored in the roots. A possible loss from the shoots to the roots is not taken into account. Perhaps the ratios were even more favourable.

Many investigators have employed themselves in the study of this process, mainly in connection with the examination of the exudation process. For this latter process the transport of water, i.e. the rate of exudation, is also important. As far as the salt secretion is concerned, it was found, as with the accumulation in the vacuoles, that the concentration of ions in the exudate may be higher than it is in the medium (Laine 1934; Hoagland and Broyer 1942; Lundegårdh 1945). This requires an active process. The problem is, whether this process is required to bring the ions from the medium into the symplasm of the root or to transport them in the symplasm, or to secrete them from the symplasm into the vessels or some combination of these processes.

As was mentioned above, Arisz made a distinction between the penetration into the cytoplasm, a further translocation and a secretion into the vacuoles. Thus, there exists a stream of ions into the vacuoles and a stream of ions circumventing the vacuoles, into the vessels (Arisz 1945). This concept is supported by the experiments of Broyer (1950). He found that if roots, having been able to absorb much bromide, were placed in a solution with radioactive bromide, the exudate is very rich in active bromide. It indicates that the bromide stored in vacuoles is retained and is hardly transferred at all.

As to the mechanism of the secretion into the vessels, equally little is known, as is the case with the accumulation in the vacuoles. It is an attractive working hypothesis to consider them together as processes related to secretion by the salt glands of salt plants (Arisz and Heykens, unpublished results). As early as 1938, Crafts and Broyer gave their hypothesis concerning the transport of ions from the medium into the vessels. On ground of anatomical features of the cortex and the stele of the roots the oxygen supply is assumed to be more favourable to the cortex than to the stele. That is why the cortical cells are able to accumulate large amounts of ions that are transported to the stele. Owing to the imperfect oxygen supply the cells surrounding the xylem vessels cannot maintain a high "accumulation level" (Wiersum 1947) so that a leakage of the ions into the vessels occurs. This line of thought can easily be applied to the special case of phosphate transport. Cells with a normal active metabolism prove to dispose of large quantities of instably bound phosphate (Kamen and Spiegelmann 1948; Green 1951) that is easily liberated so that it can be considered as if it was an inorganic phosphate. Apart from this, in experiments over the loss of phosphate, it was shown that under conditions of low metabolic activity, phosphate is readily given off. So such a leakage might easily occur as a "normal" phenomenon within the stele. The resistance to a diffusion of free anions in the symplasm might prevent the ions from being transported to cortex and medium.

It is more difficult to judge how far the hypothesis is correct as to the transport of the other ions. It also remains uncertain whether the oxygen supply of the stele is insufficient as it is obvious to assume this on ground of anatomical data. It may even be doubted as to whether a low oxygen tension is an essential condition for the loss of ions. For, with the salt glands on the leaves of halophytes a secretion also occurs. An insufficient oxygen supply seems to be very unlikely. Lundegårdh (1950) arrives at the conclusion on ground of his results with inhibitors, that the uptake into the root and the secretion into the vessels are different processes. For the uptake into and the further transport in the symplasm the anion respiration is necessary (up-hill reaction). The loss of ions into the vessels (down-hill reaction) is connected with glycolytic metabolism. Thus it is possible that there are different enzyme systems and hence differences in metabolism in the secreting cells and the absorbing cells of the cortex.

The exudation phenomenon is also studied in order to obtain some insight into the process of water intake (Kramer 1949). The main problem is whether this transport is an active or a passive one. The question, as to whether the difference in osmotic value between exudate and medium is sufficient to explain the rate of exudation, has been the object of some recent investigations (Van Overbeek 1942; Eaton 1943; Van Nie, Helder and Arisz 1950). The authors last mentioned arrived at the conclusion that the osmotic regulation is an important factor, at least in tomato plants. In this there is difference of opinion with Lundegårdh, who attaches less and less value in his latest articles to the osmotic value of the exudation sap. This difference in valuation of the osmotic component of the exudation does not involve a complete contradiction between the concepts of these authors and Lundegårdh, as has been claimed by Burström (1951). As appears from the more elaborate article of Arisz, Helder and Van Nie (1951), the importance of the salt secretion for the exudation is fully recognized. There is an intimate connection between salt secretion and water transport and a mutual influencing.

As for accumulation and growth, the transport of ions and water from the medium into the vessels depends on the sugar supply (Went 1944). The importance of the salt condition was mentioned. It points to a competition between the various processes: fixation by growth, accumulation in the vacuoles and secretion into the vessels. With a low salt condition and a low external salt concentration, a large part of the salt absorbed is retained by the roots themselves. An insufficient salt supply to the shoot will influence the activities of the roots which may lead to a better salt supply from the roots to the shoots. How far there is a direct regulating influence on the secretion into the vessels of the root is unknown.

Finally, the uptake is influenced by the loss of ions from the shoot. This loss in its turn is connected with the entire salt metabolism of the shoots. Perhaps, the processes of uptake by shoots are comparable to those by roots. If this applies, it means that one has to distinguish between entry into the cytoplasm, transport in the cytoplasm, fixation by growth processes, accumulation in the vacuoles and loss to the sieve tubes. If the uptake has been split up in such a way it will be clear that there might also be some differences. The medium of the shoot tissue is formed by the content of the xylem vessels. By means of the transpiration and exudation stream new amounts of ions are steadily supplied. During the experiments, mentioned here, the transpiration was only slight owing to the humid conditions. Guttation of the leaves was very often observed. It is not very likely that under these conditions a selective absorption occurs, for it would cause a concentration of the ions to form in the vessels. This renders a more or less passive penetration of the ions into the protoplasm more likely. The situation might be compared with roots deprived of their epidermis (Burström 1951; Sandström 1950).

With a limited consumption of the ions, absorbed in this way, a surplus arises that is transported back to the root by the phloem vessels (Biddulph 1951). The final result is a circulation of ions within the plant. For a further discussion of the principles of translocation of substances in the sieve tubes and the significance of such a circulation, one may be referred to a recent review (Arisz 1952). Whereas the salt- and sugar condition may play an equal part in these various processes in the shoot as they do in the root, the translocation to the roots may in particular be linked up with the translocation of the sugar in the sieve tubes.

THE UPTAKE BY THE INTACT PLANT

An analysis of the absorption behaviour by intact plants was the very beginning of these experiments. In explaining the course observed, the several factors and processes mentioned up till now, will have to be taken into account. As there were some hypothetical elements involved in the principles mentioned, if we have to take into account the interaction of the different processes, the hypothetical element becomes greater. A consideration of the physiology of the salt relations in the intact plant cannot be anything but speculative in nature. The discussion will therefore, be restricted to one concrete case viz. the decrease in the salt absorption when the plants are placed in darkness.

It was obvious from the experiments concerning the influence of a dark treatment and the withdrawal of carbon dioxide, that the effect of the light factor is mainly an indirect one (photosynthesis). A direct influence on the accumulation into the vacuoles was observed by ARISZ (1947). Luttkus und Bötticher (1939) assumed potassium in the leaves of maize plants to be bound to an unknown protoplasmic substance when the leaves are in the light. VAN DER BURG (1952) showed that the cessation of the potassium uptake in darkness was due to the cessation of photosynthesis. If the sugar supply stops, all energy consuming processes e.g. growth or accumulation in the vacuoles, diminish. The extent to which this happens depends on the amount of sugar avaiable, which is in its turn correlated with the salt condition. Moreover, the various processes are sensitive to the sugar supply to a variable degree. At any rate the final result is a decreased consumption of salt by the shoot. If the salt supply from the root remains the same, a surplus originates in the shoot, which together with the ions continuously liberated in the aging parts is transported back to the root. This loss of salts by the shoot is highest for high salt plants, because firstly the supply from the root is large, secondly the consumption is mainly determined by growth that is very sensitive to a dark treatment and finally the loss by the older parts is large. These salts coming from the shoots, can be expected to compete immediately with the ions of the medium. At the same time the decreased sugar supply will enhance the depressing effect on the absorption from the medium, because it can diminish the uptake from the medium into the symplasm of the root. As to the phosphate absorption, where this first stage depends on an esterification, the connection of this first stage with the sugar metabolism is very likely. To what extent it is important to other ions is difficult to say. The transport in the cytoplasm, the growth processes, the accumulation in the vacuoles and the secretion into the vessels also depend on the sugar supply. The salt and sugar condition is important again in this connection. The final result is that the uptake from the medium, in particular by high salt plants, is more sensitive to the alterations of light and darkness than that of low salt plants.

Next to the loss of salts and the diminished sugar supply from the shoots, other special factors may play a part. Hormonic influences on the growth of the shoots as well as on the roots, and as a result of this hormonic influences on the uptake are possible. It is quite unknown how far such influences exist e.g. on the secretion into the vessels, and in what way ions stored in the vacuoles are liberated and made available to the shoots also remains an unsolved problem.

As was admitted this scheme is speculative It is given in order to obtain a preliminary review of the salt relations of the intact maize plants. At the same time it may serve not only to show how complex the uptake by intact plants may be, but also to illustrate that, except for the absorption problem in its strict sense, there remain many typical physiological problems concerning the salt uptake of higher plants.

V. SUMMARY

In all experiments sets of intact maize plants were used, high salt as well as low salt ones. As a rule the phosphate uptake was determined and occasionally the nitrate uptake. In some experiments the growth was determined by tracing the development of the shoots.

The starting point was the examination of the course of the uptake of phosphate and the growth in light and darkness. Initially the uptake increases in light, in particular with low salt material. But with an intensive illumination the uptake by high salt material also increases. After some days a constant level is attained. In darkness the uptake decreases. The extent to which this occurs with low salt material depends on the degree in which the plants have been turned into a high salt condition. This can be regulated experimentally by the use of various concentrations.

The growth of the shoot increases mostly only a little during the first days of an experiment. Afterwards it remains at a constant level but shows a typical day and night rhythm in spite of constant conditions. In darkness the growth drops. Generally uptake and growth progress parallel to each other, but there are exceptions.

It appeared from analysis of the plants, that a large amount of the phosphate absorbed is transferred to the shoot. With an extremely low salt condition the amounts present in the shoot and root are almost equal. If the plants are standing on a nutrient solution, a large part is transferred to the shoot.

In explanation of the behaviour observed, the uptake from the external solution was assumed to depend on a number of physiological factors: fixation by growth processes in root and shoot; accumulation in the vacuoles; secretion into the vessels; loss from the shoots. The importance of accumulation and secretion is obvious. The effect of the loss from the shoot (as far as it can be studied from a single experiment) could not be obtained.

On the other hand growth proved to be of primary importance. In order to show this, high nitrate, low phosphate plants were grown. By lack of phosphorus, growth was checked. Some nitrate absorption was possible but it soon came to a standstill, the plants coming in

a nitrate saturated condition as a result of the daily renewal of the solutions. By phosphate supply the synthetic processes could get started. This leads on the one hand to a renewed nitrate absorption, on the other hand to the promotion of the visible growth.

All processes mentioned are connected with metabolism. That is why sugar supply can be expected to have an influence. As a matter of fact carbon dioxide-free air proved to depress the uptake in the same way as does a dark treatment. The uptake could also be enhanced by the addition of glucose to the solution. At intensive illumination it does not occur. With low salt material a prolonged dark treatment may be necessary before a clear effect of the glucose addition is obtained. Hence it is not surprising that the uptake by low salt material is less sensitive to the changing of light and darkness, than is high salt material. Perhaps, this is mainly due to the accumulation in the vacuole being less sensitive to sugar supply, since much sugar has been stored in the vacuoles (osmoregulation).

Whether there is an effect of glucose addition or not, also depends on the external phosphate concentration. It was found, in accordance with the common concepts that the relation between concentration and uptake can be represented by an adsorption isotherm (Freundlich- or Langmuir curve). The well-known "saturation phenomenon" was also obtained. If the absorption activity of the plants increases, the uptake at a lower concentration is more enhanced than at a higher one. If glucose has an enhancing effect, then the higher the concentration the larger the effect.

To explain the regularities observed, the uptake of phosphate was assumed to start by becoming bound to some specific substance which is present in a limited amount. The preliminary data concerning the inhibition of the uptake by phloridzin also points to such a phosphorylation. Following on this initial binding the phosphate is translocated inwardly the symplasm of the roots. This translocation may be influenced by glucose. Langmuir's formula proves to be of primary importance in this concept. It renders a calculation of the theoretical "saturation" value possible. In nearly all cases where a maximum rate of the uptake was found, this appeared to be lower than this theoretical "saturation" value. This must be connected to a limiting influence of the consumption.

The significance of the metabolism for the phosphate uptake is obvious. However, experiments on the rapid loss of phosphate depending on the concentration of the medium, point to a large passive permeability. The significance of active and passive processes on the anion uptake was discussed in detail. It is emphasized that in general, the various principles, factors and processes important to the uptake, do not exclude one another. Nevertheless their quantitative meaning will depend on the certain known conditions e.g. low salt condition of the plants. Next to this the nature of the anion which is absorbed, particularly the extent to which it is taken up by the cytoplasm or the extent to which it is secreted into the vacuoles, is very important.

LITERATURE CITED

Achromeiko, A. J. (1936). Über die Ausscheidung mineralischer Stoffe durch Pflanzenwurzeln. Zeitschr. f. Pflanzenernähr., Düng. u. Bodenk. *42,* 156—86.

Alberda, Th. (1948). The influence of some external factors on growth and phosphate uptake of maize plants of different salt conditions. Rec. trav. bot. néerl. *41,* 541—601.

Andel, O. M. van, W. H. Arisz, and R. J. Helder (1950). Influence of light and sugar on growth and salt intake by maize. Proc. Kon. Akad. Wet. *53,* 159—71.

Arisz, W. H. (1945). Contribution to a theory on the absorption of salts by the plant and their transport in parenchymatous tissue. Proc. Kon. Akad. Wet. *48,* 420—46.

Arisz, W. H. (1947). Uptake and transport of chlorine by parenchymatic tissue of leaves of *Vallisneria spiralis.* II. Analysis of the transport of chlorine. Ibid. *50,* 1235—45.

Arisz, W. H. (1948). Uptake and transport of chlorine by parenchymatic tissue of leaves of *Vallisneria spiralis.* III. Discussion of the transport and the uptake. Vacuole secretion theory. Ibid. *51,* 25—33.

Arisz, W. H. (1952). Translocation of organic compounds. Ann. Rev. of Plant Physiol. *3,* 109—30.

Arisz, W. H., R. J. Helder and R. van Nie (1951). Analysis of the exudation process in tomato plants. J. exp. Bot. *2,* 257—97.

Asana, R. D. (1949). The absorption of nitrogen by the sugar-cane plant at different stages of growth. Ann. of Bot. N. S. *13,* 237—40.

Biddulph, O. (1951). The translocation of minerals in plants. Mineral Nutrition of Plants. Univ. of Wisconsin Press. 261—75.

Booy, H. L. and H. P. Wolvekamp (1944). Catenary processes, master reactions and limiting factors. Biblioth. biotheor. Ser. D, *1,* 145—224.

Brandt, K. (1942). Ueber Phosphatausscheidung und Permeabilität der getrockneten Bäckerhefe. Biochem. Zeitschr. *312,* 89—99.

Briggs, G. E. and R. N. Robertson (1948). Diffusion and absorption in discs of plant tissue. New Phytol. *47,* 265—83.

Brooks, S. C. and M. M. Brooks (1941). The permeability of living cells. Protoplasma Monogr. Borntraeger, Berlin.

Broyer, T. C. (1950). Further observations on the absorption and translocation of inorganic solutes using radioactive isotopes with plants. Plant Physiol. *25,* 367—77.

Broyer, T. C. (1951). The nature of the process of inorganic solute accumulation in the roots. Mineral nutrition of plants. Univ. of Wisconsin Press, 187—249.

Broyer, T. C. and D. R. Hoagland (1943). Metabolic activities of roots and their bearing on the relation of upward movement of salts and water in plants. Amer. J. Bot. *30,* 261—73.

Bull, H. B. (1951). Physical biochemistry. John Wiley & sons, Inc. New York. Chapman & Hall Lim. London.

Burd, J. S. (1919). Rate of absorption of soil constituents at successive stages of plant growth. J. agric. Res. *18,* 51—72.

Burg, A. H. van der (1952). Influence of light on the absorption of potassium by maize plants in carbondioxide-free air. Proc. Kon. Akad. Wet. ser. *C 55*

Burström, H. (1947). A preliminary study on mineral nutrition and cell elongation of roots. Kungl. fysiogr. Sällsk. Lund Förhandl. *17.*

Burström, H. (1948). Mineral nutrition of plants Ann. Rev. Biochem. *17,* 579—99.

Burström, H. (1949). Studies on growth and metabolism of roots. I. The action of n-diamylacetic acid on root elongation. Physiol. Plant. *2,* 197—209.

Burström, H. (1951). Mineralstofwechsel. Fortschr. d. Bot. *13,* 250—68

Burström, H. (1951). The mechanism of ions absorption. Mineral nutrition by plants. Univ. of Wisconsin Press, 251—260.

Crafts, A. S. and T. C. Broyer (1938). Migration of salts and water into xylem of the roots of higher plants. Amer. J. Bot. *25,* 529—35.

Davies, R. E. and A. G. Ogston (1950). The mechanism of acid secretion by gastric mucosa and by other tissues. Bioch. Journ. *46,* 324—33.

Deleano, N. T. und M. J. Andreesco, (1932). Beiträge zum Studium der Rolle und Wirkungsweise der Mineral- und organischen Stoffe im Pflanzenleben. I. Der quantitative Stoffwechsel der Mineral- und organischen Substanzen in der Salix fragilis-blättern während ihre Entwicklung. Beitr. z. Biol. d. Pflanzen *19*, 249—84.

Eaton, Scott V. (1949). Effects of phosphorus deficiency on growth and metabolism of sunflower. Bot. Gaz. *110*, 449—64.

Eaton, Scott V. (1950). Effects of phosphorus deficiency on growth and metabolism of Soy bean. Bot. Gaz. *111* 426—36.

Eaton. F. M. (1943). The osmotic and vitalistic interpretations of exudation. Amer. J. Bot. *30*, 663—74.

Franco, C. M. and W. E. Loomis (1947). The absorption of phosphorus and iron from nutrient solutions. Plant Physiol. *22*, 627—34.

Freeland R. O. (1937). Effect of transpiration upon the absorption of mineral salts. Amer. J. Bot. *24*, 373—74.

Frey-Wyssling, A. (1948). Submicroscopic morphology of protoplasm and its derivatives. Elsevier Publ. Comp. Inc. Amsterdam.

Frey-Wyssling, A., A. K. Mühlethaler und R. W. G. Wyckoff (1948). Microfibrillenbau der pflanzlichen Zellwände. Experientia *4*, 475—76.

Gale, E. F. (1947). The assimilation of amino acids by Bacteria. 1. The passage of certain amino acids across the cell wall and their concentration in the internal environment of Streptococcus faecalis. J. gen. Microbiol. *1*, 53—76.

Green, D. E. (1951). The cyclophorase complex of enzymes. Biol. Rev. *26*, 410—55.

Gregory, F. G. (1937). Mineral nutrition of plants. Ann. Rev. Biochem. *46*, 557—78.

Haurowitz, F. (1948). Fortschritte der Biochemie 1938—47. C. Karger Basel, New York.

Helder, R. J. (1951). Growth as a determining factor for the intake of anions by maize plants. Proc. Kon. Akad. Wet. ser. C *54*, 275—86.

Hinshelwood, C. N. (1946). Chemical kinetics of the bacterial cell. Oxford Univ. Press, London.

Hoagland, D. R. (1948). Lectures on the inorganic nutrition of plants. Chronica Bot. Comp. Sec. print. Waltham Mass.

Hoagland, D. R., and T. C. Broyer (1936). General nature of the process of salt accumulation by roots with description of experimental methods. Plant Physiol. *11*, 471—507.

Hoagland, D. R. and T. C. Broyer (1942). Accumulation of salt and permeability in plant cells. J. gen. Physiol. *25*, 865—80.

Höber, R. (1945). Physical chemistry of cells and tissues. J. & A. Churchill Ltd. London.

Honert, T. H. van den (1933). The phosphate absorption by sugar cane. Leiden.

Honert, T. H. van den (1936). Beperkende factoren bij de phosphaat opname (with English translation). Leiden.

Hornberger, R. (1882). Chemische Untersuchungen über das Wachstum der Maispflanze. Landw. Jahrb. *11*, 359—523.

Humphries, E. C. (1950). The absorption of ions by excised root systems. I. Apparatus and preliminary experiments. J. exp. Bot. *1*, 282—300.

Humphries, E. C. (1951). The absorption of ions by excised root systems. II. Observations on roots of barley grown in solutions deficient in phosphorus, nitrogen or potassium. J. exp. Bot. *2*, 344—79.

Jacobson L. and R. Overstreet (1947). A study of the mechanism of ion absorption by plant roots using radioactive elements. Amer. J. Bot. *34*, 415—20.

Jacobson L., R. Overstreet, H. M. King and R. Handley (1950). A study of potassium absorption by barley roots. Plant. Physiol. *25*, 639—47.

Jennie, H. and R. Overstreet (1939). Surface migration of ions and contact exchange. J. Phys. Chem. *43*, 1185—96.

Kamen, M. D. and S. Spiegelman, (1948). Studies on the phosphate metabolism of some unicellular organisms. Cold Spring Harbor Symposia on quantitative Biology *13*, 151—63.

Knowles, F. and J. E. Watkin (1931). The assimilation and translocation of plant nutrients in wheat during growth. J. Agr. Sci. *21*, 612—37.

KRAMER, P. J. (1949). Plant and soil water relationships. McGraw–Hill Book Co. Inc. New York.

LAINE, T. (1934). On the absorption of electrolytes by the cut roots of plants and the chemistry of plant exudation sap. Acta Bot. Fennica. *16*, 1—64.

LOOMIS, W. E. and CH. A. Shull (1937). Methods in plant physiology. McGraw–Hill Book Comp. Inc. New York, London.

LUNDEGÅRDH, H. (1945). Absorption, transport and exudation of inorganic ions by the roots. Ark. f. Bot. *32 A* (12), 1—139.

LUNDEGÅRDH, H. (1947). Mineral nutrition of plants. Ann. Rev. Bioch. *16*. 503—28.

LUNDEGÅRDH, H. (1950). The translocation of salts and water through wheat roots. Physiol. Plantarum *3*, 103—51.

LUTTKUS, L. und R. BÖTTICHER (1939). Über die Ausscheidung von Aschenstoffen durch die Wurzeln. Planta *29*, 325—40.

MACHLIS, L. (1944). The respiratory gradient in barley roots. Amer. J. Bot. *31*, 281—82.

MASON, T. G. and E. J. MASKELL (1931). Further studies on transport in the cotton plant. I. Preliminary observations on the transport of phosphorus, potassium and calcium. Ann. Bot. *45*, 125—73.

MASON, T. G. and E. PHILLIS (1945). The effect of ringing and of transpiration on mineral uptake: A reply to criticism. Ann. Bot. N.S. *9*, 345—51.

MAXIMOW, N. H. (1938). Plant Physiology. McGraw–Hill Book Co. London.

MCINTYRE, G. A. and R. F. WILLIAMS (1949). Improving the accuracy of growth indices by the use of ratings. Austr. J. sci. Res. ser. B *2*, 319—45.

MILLERD, A., J. BONNER, B. AXELROD, and R. BANDURSKI (1951). Oxidative and phosphorylatic activity of plant mitochondria. Proc. Nat. Acad. Sci. *37*, 855—62.

MOORE, R. F. (1949). Downward translocation of phosphorus in separated maize roots. Amer. J. Bot. *36*, 166—69.

MÜHLETHALER, A. K. (1950). Electron microscopy of developing plant cell walls. Biochim. Biophys. Acta *5*, 1—9.

NANCE, J. F. (1949). Inhibition of salt accumulation in excised wheat roots by 2,4-dichlorophenoxi acetic acid. Science *109* (2825), 174—76.

NELSON, A. (1946). Principles of agricultural Botany. Nelson and Son Ltd. London.

NICKERSON, W. J. (1949). Dependence, in yeast, of phosphate uptake and polymerization upon the occurrence of glucose polymerization. Experientia V, 202—3.

NIE, R. VAN, R. J. HELDER and W. H. ARISZ (1950). Ion secretion into the xylem and osmotic regulation of exudation. Proc. Kon. Akad. Wet. *53*, 567—75.

OLSEN, C. (1938). Iron absorption and chlorosis in green plants. C. R. trav. Laborat. Carlsberg sér. chim. *21*, 15—52.

OLSEN, C. (1938). Experiments with different quantities of iron salts given to maize in water culture. Ibid. *21*, 301—14.

ÖSTERLIND, S. (1951). Anion absorption by an alga with cyanide resistent respiration. Physiol. Plant. *4*, 528—34.

OVERBEEK, J. VAN (1942). Water uptake by excised root systems of the tomato due to non-osmotic forces. Amer. J. Bot. *29*, 677—83.

OVERSTREET, R. and T. C. BROYER (1940). The nature of absorption of radioactive isotopes by living tissues as illustrated by experiments with barley plants. Proc. Nat. Acad. Sci. *26*, 16—24.

PAAUW, F. VAN DER (1948). Absorption of phosphate and nitrogen, assimilation and structural distribution in potatoes grown under varied phosphate conditions. Versl. Landb. Onderz. *54*, 3.

PARKER, F. W. and J. F. FUDGE, J. F. (1927). Soil-phosphorus studies. I. The colorimetric determination of organic and inorganic phosphorus in soil extracts and the soil solution. Soil Science *24*, 109.

PERNER, E. S. (1952). Zellphysiologische und zytologische Untersuchungen über den Nachweis und die Lokalisation der Cytochrom-Oxydase in Allium Epidermiszellen. Biol. Zentralbl. *71*, 43—69.

PHILLIS, E. and T. G. MASON (1940). The effect of ringing on the upward movement of solutes from the root. Ann. Bot. N.S. *4*, 635—44.

PHILLIS, E. and T. G. MASON (1940). The effect of ringing and of transpiration on mineral uptake. Ibid. *4*, 645—50.

PREVOT, P. and F. C. STEWARD (1936). Salient features of the root systems relative to the problem of salt absorption. Plant Physiol. *11*, 509—34.

RICHARDS, F. J. and W. G. TEMPLEMAN (1936). Physiological studies in plant nutrition. IV. Nitrogen metabolism in relation to nutrient deficiency and age in leaves of barley. Ann. Bot. *50*, 367—402.

ROBERTSON, R. N. (1940). Studies on the metabolism of plant cells. I. Accumulation of chlorides by plant cells and its relation to respiration. Austr. J. exp. Biol. Med. Sci. *19*, 264—78.

ROBERTSON, R. N. (1950) Presidential address. Proc. Linn. Soc. N. South Wales *75*.

ROBERTSON, R. N. (1951) Mechanism of absorption and transport of inorganic nutrients. Ann. Rev. Plant Physiol. *2*, 1—24.

ROBERTSON, R. N. and J. S. TURNER (1945). Studies in the metabolism of plant cells. III. The effect of cyanide on the accumulation of potassium chloride and on respiration; the nature of the salt respiration. Austr. J. exp. Biol. Med. Sci. *23*, 63—73.

ROBERTSON, R. N., M. J. WILKINS and D. C. WEEKS (1951). Studies in the metabolism of plant cells. IV. The effect of 2,4 dinitrophenol on salt accumulation and salt respiration. Austr. J. Sci. Res. *B 4*, 248—64.

ROELOFSEN, P. A. and A. L. HOUWINK (1951). Cell wall structure of staminal hairs of *Tradescantia virginica* and its relation with growth. Protoplasma *40*, 1—22.

ROTHSTEIN, A. and R. MEIER (1948. The relationship of the cell surface to metabolism. I. Phosphatases in the cell surface of living yeast cells. J. cell. Comp. Physiol. *32*, 77—95.

ROUSCHAL, E. und S. STRUGGER (1940. Der fluoreszenz optisch-histo-chemische Nachweis der kutikulären Sekretion und des Salzweges im Mesophyll. Ber. d. bot. Ges. *58*, 50—69.

RUFZ DE LAVISON, J. DE (1910). Du mode de pénétration de quelques sels dans la plante vivante. Role de l'endoderme. Rev. Gen. Bot. *22*.

SABININ, D. A. (1925). On the root system as an osmotic apparatus. Bull. Inst. Recherche biol. Univ. Perm *4*, suppl. 2, 129—36.

SANDE BAKHUYZEN, H. L. VAN DE (1937). Studies on wheat grown under constant conditions. Stanford Univ. Press California.

SANDSTRÖM, B. (1950). The ion absorption in roots lacking epidermis. Physiol. Plant. *3*, 496—585.

SAYRE, J. D. (1948). Mineral accumulation in corn. Plant Physiol. *23*, 267—81.

SCHMIDT, O. (1936—37). Die Mineralstoffaufnahme der höhere Pflanze als Funktion einer Wechselbeziehung zwischen inneren und äusseren Faktoren. Zeitschr. Bot. *30*, 289—334.

SCHUFFELEN, A. C. (1948). Growth substance and ion absorption. Plant and Soil *1*, 121—26.

SCHWAB, G. M. (1941). Handbuch der Katalyse. III. Biokatalyse. Springer—Verlag Wien.

SHAPIRO, B. (1947). The mechanism of phloridzin glucosuria. The biochem. J. *41*, 151—54.

SNELL, F. D. and C. T. SNELL (1936). Colorimetric methods of analysis. Chapman and Hall Ltd. London.

STEINBACH, H. B. (1951). Permeability. Ann. Rev. Plant Physiol. *2*, 323—42.

STEWARD, F. C. (1943). The effect of ringing and transpiration on mineral uptake. Ann. Bot. N.S. *7*, 89—92.

STEWARD, F. C. (1935). Mineral nutrition of plants. Ann. Rev. Biochem. *4*, 519—44.

STREET, H. E. and J. S. LOWE (1950). The carbohydrate nutrition of tomato roots. II. The mechanism of sucrose absorption by excised roots. Ann. Bot. N.S. *14*, 307—29.

THOMAS, W. (1933). Absorption, utilization and recovery of nitrogen, phosphorus and potassium by apple trees grown in cylinders and subjected to differential treatment with nutrient salts. J. agric. Res. *47*, 565—81.

TSAO, TSUNG-HSUN G. S. RABIDEAU and W. G. WHALEY (1950). The phosphorus uptake of Andropogon ischaemum L. at various stages of development. Plant Physiol. *25*, 653—65.

WALKLEY J. (1940). Protein synthesis in mature and senescent leaves of barley. New Phytolog. *39*, 362—69.

WATSON R. and A. H. K. PETRIE (1940). Physiological ontogeny in the tobacco plant. IV. The drift in nitrogen content of the parts in relation to phosphorus supply and topping with an analysis of the determination of ontogenetic changes. Austr. J. exp. Biol. Med. Sci. *18*, 313.

WEEKS D. C. and R. N. ROBERTSON (1950). Studies in the metabolism of plant cells. VIII. Dependence of salt accumulation and salt respiration upon the cytochrome system. Austr. J. Sci. Res. *B 3*, 487—500.

WENT, F. W. and M. CARTER (1948). Growth responce of tomatoplants to applied sucrose. Amer J. Bot. *35*, 95—106.

WENT, F. W. (1944). Plant growth under controlled conditions. III. Correlations between various physiological processes and growth in the tomato plant. Amer. J. Bot. *31*, 597—618.

WIERSUM, L. K. (1947). Transfer of solutes across the young root. Rec. trav. bot. Néerl. *41*, 1—79.

WILFARTH, H., H. RÖMER und G. WIMMER (1906). Über die Nährstoffaufnahme der Pflanzen in verschiedenen Zeiten ihres Wachstums. Landw. Versuchs Stat. *63*, 1—70.

WILLIAMS, R. F. (1938). Physiological ontogeny in plants and its relation to nutrition. IV. The effect of phosphorus supply on the total protein- and soluble nitrogen contents and water content of the leaves and other plant parts. Austr. J. exp. Biol. Med. Sci. *16*, 65—83.

WILLIAMS, R. F. (1948). The effects of phosphorus supply on the rates of intake of phosphorus and nitrogen and upon certain aspects of phosphorus metabolism in gramineus plants. Austr. J. sci. Res. ser. *B* 1, 333—61.

WILSON, C. C. and P. J. KRAMER (1949). Relation between root respiration and absorption. Plant Physiol. *24*, 55—59.

WOOD, R. K. S., A. H. GOLD and T. E. RAWKINS (1952). Electron microscopy of primary cell walls treated with pectic enzymes. Amer. J. Bot. *39*, 132—33.

WOODFORD, E. K. and F. GREGORY (1948). Preliminary results obtained with an apparatus for the study of salt uptake and root respiration of whole plants. Ann. Bot. N.S. *12*, 335—70.

KJELLBERGIODENDRON AND WHITEODENDRON, MALAYSIAN MYRTACEAE – LEPTOSPERMOIDEAE METROSIDERINAE

BY

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During the past decades it has become clear that the *Myrtaceae* of Malaysia are taxonomically of a far more varied character than they appeared to phytographers of the 19th century. The genus *Eugenia* s.l. (the Syzygium-complex and its segregates) now rivals, in number of species, the genus *Eucalyptus* in Australia. Many of the Australian-New Caledonian genera have been shown to possess representatives in Malaysia (*Myrtella*, *Mearnsia*, *Syncarpia*, *Agonis*, *Fenzlia*, *Myrtus*, *Mooria*) and others are far richer in species than anticipated (*Metrosideros*, *Decaspermum*, *Tristania*, *Melaleuca* (7), *Xanthostemon*) according to MERRILL & PERRY (5).

However, there is also a manifestly endemic element, specially in the East Malaysian province. *Xanthomyrtus* Diels (2) is now a fairly large genus occurring from Mt Kinabalu eastward, culminating in a large number of species in the New Guinean highlands. *Octamyrtus* Diels now contains six species (9). The late Mr C. T. WHITE has recently described two other endemic genera, viz. *Eucalyptopsis* from Buru & New Guinea (9, p. 139) and *Basisperma* from New Guinea (8). In 1936 Dr BURRET, of Berlin, described the singular genus *Kjellbergiodendron* from Celebes (1).

But also Borneo, that great centre of plant distribution in West Malaysia does seem to contain still unrecognized novelties in the *Myrtaceae* which seem of extraordinary interest to Myrtaceous taxonomy as is shown by the new genus described below.

It shows a most remarkable though unmistakable resemblance to *Kjellbergiodendron* but in contrast to it it is capsular-fruited, thus challenging the familiar, still current division of the family in fleshy-fruited *Myrtoideae* and capsular-fruited *Leptospermoideae*. The case is so strong, that — for separating these two genera — I assume this division to be artificial, whatever the consequences will be. *Kjellbergiodendron*, *Whiteodendron* and *Basisperma* belong together to the Tristania-complex of the Leptospermoideae. I feel strengthened by the remarks made by BURRET who already pointed to the aberrant place of *Kjellbergiodendron* in the Myrtoideae and to its affinity with *Tristania*. *Whiteodendron* gives the final clue to this relation.

I have to tender my sincere thanks to the Regius Keeper of the

Botanic Gardens at Edinburgh and the Director of the Royal Botanic Gardens, Kew, for having the privilege to examine some types of Tristanias.

Whiteodendron gen. nov.

Tristaniae affine sed recedit adelphiis filamentorum basi in tubum connatis; fructu uniloculari; semine unico magno. (Fig. 1.)

Arbor glabra, haud magna, omnibus partibus glandulosa; ramulis teretibus, cortice haud in Tristaniae modo exfoliante. Gemma terminalis cuspidiformis longa teres, falcata, acuta.

Folia spiraliter ordinata, manifeste obliqua, obovato-oblonga, integerrima basi angustata in petiolum perbreve, crassum in sicco transverse rugulosum, apice acutiuscula obtusave; costa robusta, facie inferiore prominens, supra leviter canaliculata; nervi laterales numerosissimi paralleli cum costa angulum ± 60° metientem efformantes, apice connati nervo intramarginali duplici.

Flores magni, 5-meri, in cymas terminales axillaresque pedunculatas dispositi, paniculam terminalem foliatam efformantes; pedunculi et rachides inflorescentiae complanati, crassi; bracteae jam ante anthesin delabentes (cicatrices tantum visae); pedicelli perspicui articulati; bracteolae deficientes vel flori valde proximae; alabastra globosa; calycis tubus late obconicus; ovarium apice leviter convexum, basi abrupte in stipitem longum contractum; calycis segmenta in praefloratione imbricata, integerrima late rotundata, latiora quam longa, persistentia; petala quincuncialia in alabastro cucullatim imbricate, deinde plana, basi lata affixa, magna, obovata, dense glandulosa, decidua; stamina numerosissima, connata in 5 adelphia magna oppositipetala; adelphia in alabastro, incurva, basi in tubum conspicuum annuliforme connata; filamenta tum in margine ut in facie interiore adelphiorum filiformia; antherae parvae, medio dorso affixae; thecis rima longitudinali dehiscentibus. Ovarium inferum, 3-loculare, apice leviter convexum, calycis tubo totum adnatum; stylus brevis, tenuiter filiformis; stigma punctiforme; placentae in quoque loculo ovarii basi approximatae, multi-ovulatae; uno ovulo tantum excrescente ceteris abortivis, in fructu tamen perspicabilibus; capsula fere tota superior, 1-locularis, tenuiter duro-coriacea, fere pro dimidia parte 3-valvis, extus subverrucosa, intus nitide straminea; semen unicum, basale oblique affixum, inde et ipsum obliquum, magnum, late ellipsoideo-globosum, notatum 3-costulis tenuibus cum valvis capsulae alternantibus, praeterea interdum cum 3 sulcis levibus, valvis oppositis; testae crassae, durae, nitidae stratum intimum extimumque tenues, medium spongioso-suberosum, crassum; cotyledones inaequalissimae, altera (exterior) crassissima, alteram (interiorem) tenuem induplicatam amplectens; plumula terminalis robusta.

Dedicated to the memory of our dear friend, the late MR C. T. WHITE, Government Botanist of Queensland, who, in undisputed authority, few weeks before his lamented death, had agreed to revise the capsular-fruited Myrtaceae for the Flora Malesiana.

By its capsular fruit and phalanged stamens the new genus doubtless

belongs to the Leptospermoideae—Metrosiderinae in the affinity of Tristania sect. Lophostemon to which it was, in absence of fruit, referred by Sir WILLIAM WRIGHT SMITH, who already observed its unique position within the genus Tristania.

Few-seeded fruits are in this group very rare. C. T. WHITE described (8) them from the genus *Basisperma* (New Guinea). Though this genus certainly belongs in the same affinity it is radically different from *Whiteodendron* by its habit, its equal-sided leaf with one intra-marginal nerve, its superior 2-celled ovary and 2-seeded fruit, and by a very different type of androecium which consists of c. 12 stamens in a not distinct phalanx before each petal and apparently no staminal tube. The stem-tip is undescribed and not developed in the duplicate specimen available to me.

However, there is another genus which is unmistakably closely allied, i.e. *Kjellbergiodendron* Burret (1). The set of conformable characters includes a remarkable resemblance in habit, a distinct though shorter, slightly curved branch-tip, an inclination to oblique leaves, and exactly the same size and structure of the flowers with synadelphous phalanges save the ovary which is 2-celled and inferior, the ovules being attached in the middle of the dissepiments. It has also one big seed with thick cotyledons, and the same coarse flattened forked peduncles and stalks, and mode of branching.

The fruit of *Kjellbergiodendron*, however, is fleshy and indehiscent, by which character it belongs to the Myrtoideae. This seems a quite unnatural position and I feel strengthened in this by the remark of BURRET himself who observed that *Kjellbergiodendron* reminds strongly of the Leptospermoideae, specially of *Tristania* sect. *Lophostemon* and that it is aberrant in the Myrtoideae both by its spirally arranged leaves and its peculiar phalanges.

Now we know the characters of the fruit of *Whiteodendron*, I have not the slightest hesitation to refer *Kjellbergiodendron* to the Leptospermoideae where it apparently represents a derivate of Tristaniaceous stock.

We have here to consider that the two differences between *Kjellbergiodendron* and *Whiteodendron* viz. resp. a fleshy wholly inferior fruit against a capsular nearly superior fruit may not be uncorrelated, as an extra, thick, fleshy layer of receptacle-derived calycinal tissue will prohibit or anyhow not facilitate splitting of a principally capsular fruit. This is also observed in Tristania where the calycinal tissue encloses the capsule in different species to various degrees but in none of the species the valves extend their splitting over the calyx! As a matter of fact it is remarkable that there are no Myrtaceae known to me which show both a wholly inferior fruit and at the same time a dehiscent fleshy fruit (including the fruiting calyx). This correlation diminishes the taxonomic importance of capsular against fleshy fruits.

These considerations do not lead to a topsyturvy of the current subfamily division of the Myrtaceae, though it is possible that exceptional cases comparable to the present one may occur elsewhere in the family.

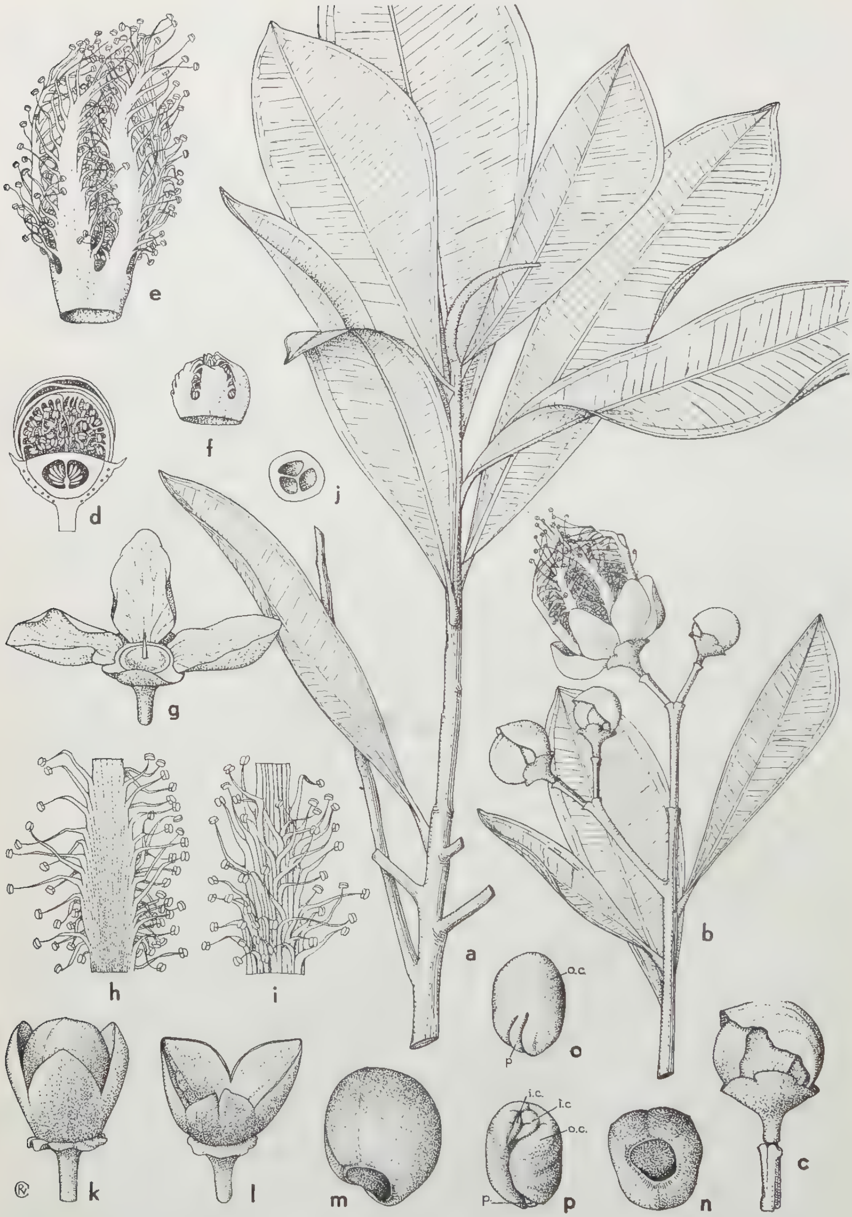

Fig. 1. Whiteodendron moultonianum (W. W. Sm.) Steen. *a*. Twig, *b*. part of inflorescence, *c*. bud, *d*. bud in section, *e*. androecium, *f*. androecium in bud, *g*. flower beyond anthesis with only 3 petals, *h*. part of phalange, outer side, magn., *i*. ditto, inner side, *j*. bottom of ovary in cross section, *k*. opened fruit with protruding seed, *l*. ditto, without seed, *m*. seed with oblique base, *n*. seed, basal view showing hilum, *o*. embryo (p = plumula, o.c. = outer cotyledon), *p*. ditto, other side (i.c. = folded inner small cotyledon). *a* and *k*—*o* after Beccari P. B. 3017, others after Beccari 879. *a*—*b* × $\frac{3}{4}$, *c*—*g*, *j*—*p* × $1\frac{1}{2}$.

Kjellbergiodendron is certainly more closely related to *Whiteodendron* than to any other genus of the group; both seem 1-seeded, synadelphous derivates from the Tristania complex in which *Whiteodendron* is still more close to *Tristania* than is *Kjellbergiodendron*.

The exact position of both genera is still to be considered; both show petals with a distinctly broad base which they share with the valvate Eucalyptinae and thus stand in contrast to the unguiculate-petalled Metrosiderinae.

Whiteodendron moultonianum (W. W. Sm.) comb. nov. — *Tristania moultoniana* W. W. Smith, Not. R. Bot. Gard. Edinb. 8 (1915) 328.

Rami cinerascentes, robusti; foliorum cicatrices suborbiculares, ± 3 mm diam. Folia omnia in apicibus ramulorum conferta, obovato-lanceolata, 7—18½ cm longa, 2½—6 cm lata, inaequilatera, parte dimidia altera lanceolato-elliptica, altera rhombeo-obovata; folia suprema parviora; nervi laterales utrinque 20—30; primariis aeque crassis ac secundariis, supra parum, infra vix prominentibus; petiolus 1—4 mm longus. Panicula 5—10 cm longa, composita simplexve; pedunculi 2—4½ cm longi; dichotomi; pedicelli ± ½ cm; calycis tubus planus, denique patelliformis, 5—7 mm diam; inferne abrupte constrictus in basin stipitiformam 3—4 mm (in fructu 8 mm) longam. Sepala ± 1 mm longa, ± 3 mm lata; calyx sub fructu vix ampliatus, glandulas verruciformes ferens; petala sub anthesi late elliptica, ± 10 mm longa, 6—7 mm lata, plana, membranaceo-marginata; tubus stamineus 3—4 mm longus, phalangibus ± 2 cm longis, filamentorum partes liberae usque ad 6 mm longae antherae ¼—⅓ mm; stylus 1½ mm. Fructus magnus ellipsoideus, ± 1½ cm longus, ± 1 cm latus, cito dehiscens; valvis suborbiculari-triangularibus, acutis, 6—8 mm longis latisque. Semen et fructu protuberans, ± 10 mm longum, ± 8 mm latum, subovoideum, in sicco nitide eburneum, hilum depressum, 3—4 mm diam; testa 1½—2 mm crassa, embryo ± 8 mm longus, ± 5 mm latus.

Sarawak. Swampy country, Nov. 21, 1913, Native collector 172 (typus, Herb. Edinb., Herb. Kew.), fl. red. Kuteing (prob. Kuching), Oct. 1865, O. Beccari P. B. 879 (= sh. no. 3818, Herb. Flor., in liquid tube no. 269), rather small tree, fl.; ibid. Dec. 1866, O. Beccari P. B. 3017 (= sh. no. 3819, Herb. Flor.), tree, vern. bilian sipi, fr.; Ragiato di Sarawak (vicinity of Sarawak), Aug. 1867, Bintulu, close to the sea, O. Beccari P. B. 3704 (= sh. no. 3821, Herb. Flor.), tree, flower white, fl.; Mattang, Sept. 1865, O. Beccari P. B. 628 (= sh. no. 3820, Herb. Flor.), young buds; Native collector 817 (for Bur. Sci. Manila), dupl. H. L. B., without number and date (distributed as Tetram(er)ista sp.), fl.

Though the Beccari collections were apparently not distributed, various herbaria will be in possession of the native collector no. 817 which was distributed as Tetram(er)ista sp.

The colour of the flowers is cited as "red" in the type specimen which possibly refers to flowers post anthesim, whereas the white

colour cited by Beccari possibly refers mainly to the phalanges. The exocarp and endocarp are at last separating in the herbarium.

Kjellbergiodendron Burret

Both species distinguished by Burret (1) were collected and described long before the genus was established. The first sheet was, of course, collected by O. Beccari in July 1874 near Kendari in Southeast Celebes. This was later described by Ridley as *Tristania anacardifolia* Ridl. (6, p. 39). In 1894—95 Koorders collected a

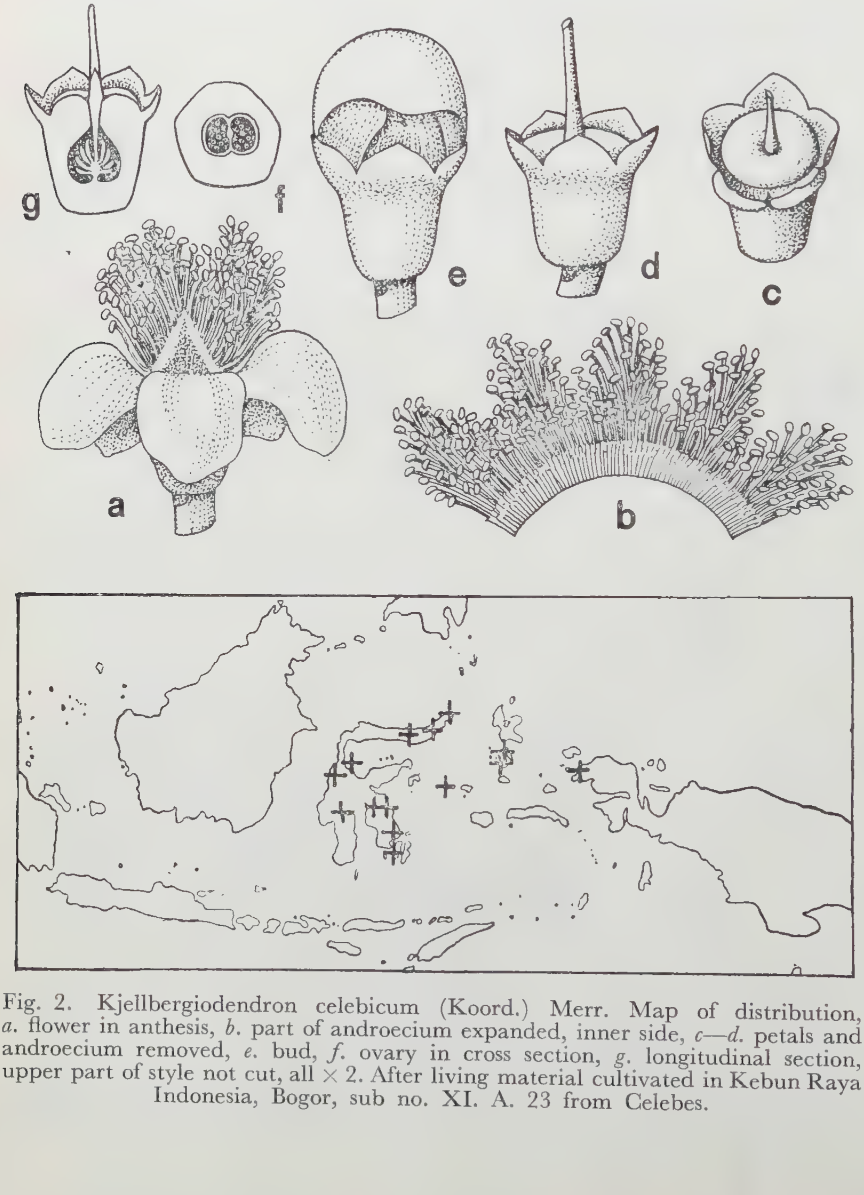

Fig. 2. Kjellbergiodendron celebicum (Koord.) Merr. Map of distribution, *a.* flower in anthesis, *b.* part of androecium expanded, inner side, *c—d.* petals and androecium removed, *e.* bud, *f.* ovary in cross section, *g.* longitudinal section, upper part of style not cut, all × 2. After living material cultivated in Kebun Raya Indonesia, Bogor, sub no. XI. A. 23 from Celebes.

species in Northeast Celebes and described it as *Xanthostemon celebicus* Koord. (4, p. 637). Its identity was independently found by me at Bogor about 1940 and by Dr Merrill in 1951 when he checked the revision by Gugerli (3).

Hitherto the genus has only been recorded from Celebes, but additional material was collected by the Forest Service in Indonesia in some of the Moluccas (see the map). Most sheets were distributed either as "Xanthostemon", as "Myrt." or as "Myrt. gen. nov.", and for the convenience of herbaria possessing duplicate specimens distributed by the Herbarium Bogoriense, the numbers have been cited below.

The species distinguished by Burret are not very well separated in the Herbarium, as their main distinction lies in the fruit which is small in one and large in the other species.

However, though the fertile material at hand is not very copious, it appears that one number (Cel. II/334) contains both small and large fruits; in the small and certainly very immature ones an appreciably developed embryo is already present. I assume that the full growth of the fruit takes some time and that the difference in size does not yield a specific character.

The same can be said about the size and shape of the leaves which are very variable; in the big series of specimens assembled gradually through the activity of the Forest Service in Indonesia all intergrades are present. The smallest leaves are found in no. bb. 5002 measuring 4½—8 × 2½—3 cm, the largest are 27 × 11½ cm (in the cited Beccari number; both sheets consists of fertile material).

Also the size of the inflorescence shows some variation viz. from 6 to 13 cm.

In immature specimens the buds are decidedly smaller and appear not full-grown.

After ample consideration I have come to the conclusion that only one species is represented, the synonymy of which is given below.

Kjellbergiodendron celebicum (Koord.) Merr. J. Arn. Arb. 33 (1952) 162. — *Xanthostemon celebicum* Koord. Minah. (1898) 637, 465; Koord.-Schum. Syst. Verz. Abt. iii, 1 (1914)96. — *Tristania anacardifolia* Ridl. J. Bot. 68 (1930) 39, syn. nov. — *Kj. limnogeiton* Burret, Notizbl. Berl.-Dahl. 13 (1936) 103, fig. 5. — *Kj. heilogeiton* Burret, l.c.

Celebes. Manado distr.: Koorders 18960, 19289, 19288 (sterile and doubtful, distributed as Tristania celebica Koord. nom. nud.), 18544, 18962, 18964, 18240, 19302, 18305, 18322, 18321, 18960, 18097, 18192; Bolaäng Mongondow distr.: Pusian, bb. 33108, vern. tombojowan; Gorontalo distr.: Buhu, bb. 19646, vern. tanna lomongo ohule; Donggala distr.: Parigi, bb. 18800, Donggala, bb. 17634, vern. kembanga golaii; Palopo & vicinity: Morante, bb. 20895; Malili distr.: Usu, Cel. II/485, vern. langara, or pude bulu, Cel. II/240—241—242—243, Maholona, bb. 19820, Cel. II/149, vern. langara, Cel. II/353, vern. pude tauru, La Roua, bb. 1836, id. 1890, id. 1854, Cel II/334, vern. tuwumea, or tanru, Tolé, bb. 26286; Kendari distr.: Lepo Lepo, Beccari sh. no. 3807 and 3808 (Herb. Flor.), Wawasungu, bb. 5002, vern. tembeüwa. Other bb. numbers are 8456, 13547.

Also cultivated in the Kebun Raya Indonesia, Bogor, sub no. XI. A. 23.

Muna Island (SW. Celebes). Raha distr., Raha, bb. 21097, Lamanu, bb. 20756, Labunti, bb. 4187, vern. timbeüwa, Barangka, vern. karasie.

Moluccas. Sula Islands (E. of Celebes). Taliabu Island, Tg. Waehaja, Atje (Hulstijn) 285.

Batjan, bb. 16467.

Halmaheira. Weda distr., Tiloppe, bb. 24838, vern. timil.

In some places *Kjellbergiodendron* seems to be a quite common tree, e.g. in the Malili forests. All localities are situated below 300 m, both in secondary and primary forest; sometimes its occurrence is characterized as common, sometimes as "spread" or rather rare. Its size is rather variable; it may vary from a small tree to one of moderate height (total height 15—32 m, clear bole 5—20 m, diam. 30—60 cm). Flowers have been found in Jan., March to June, and Oct.; fruits in May and June.

Of the cited living plant in the Botanic Gardens the following notes were made (cf. fig. 2). Twigs cinnamon-coloured. Calyx tube yellowish-green, tinged reddish below the lobes. Base of petals rosa in bud, reflexed in anthesis, inner side white. Phalanges with a reddish centre and base, filaments and anthers yellowish. Top of ovary convex yellowish. Style pink. Ovary 2-celled; placenta near the base of the dissepiment, swollen; ovules numerous, elongate, ascending.

REFERENCES

1. Burret, M., in Notizbl. Berl.-Dahl. *13* (1936) 101—106.
2. Diels, L., in Bot. Jahrb. *57* (1922) 362.
3. Gugerli, K., Monographie der Myrtaceengattung Xanthostemon. Inaug. Diss. Zürich 1940.
4. Koorders, S. H., Med. 's Lands Plantentuin no. *xix* (1898). — Abbrev. "Koord. Minah."
5. Merrill, E. D. & L. M. Perry, J. Arn. Arb. *23* (1942) 233-297.
6. Ridley H. N. in J. Bot. *68* (1930) 10—17, 33—39.
7. Steenis, C. G. G. J. van, in Tectona *31* (1938) 899.
8. White, C. T., in J. Arn. Arb. *23* (1942) 84.
9. White, C. T., ibid. *32* (1951) 143.

PS. In 1948 Mr Pleyte collected *Kjellbergiodendron* several times in the Island of Misool; the locality in the Island of Sorong, West New Guinea, indicated on the map should, however, be omitted.

NOMENCLATURAL NOTE ON THE GENUS BUCKLANDIA R.BR. (HAMAM.)

BY

C. G. G. J. VAN STEENIS

(Received June 18th, 1952)

The generic name *Bucklandia* R.Br. has mostly been cited ex Wall. Cat. (1830) no 7414. However, this is a nomen nudum which was validated ex Griff. (in As. Res. 19, 1, 1836, p. 94, t. 13—14).

However, the same name had been given in honour of the same person (William Buckland, an eminent British geologist) already in 1825 by Presl in Sternberg's folio book "Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt" which (acc. to the title page) consists of four parts, with a principally German text. The Leyden copy contains next to that a Latin-paged part covering xlii pages + index in which many new genera and species of fossil plants have been described manifestly edited separately and bearing the title "Tentamen florae primordialis". This part is mentioned by Pritzel (p. 306*a*) to belong to this work. In palaeobotanical literature it is apparently ascribed to Presl, and the appertaining novelties are provided with the author's name "Presl in Sternb." The introduction of this Latin descriptive part is dated "Pragae 27. Aprilis 1825", and it is generally accepted to have appeared in 1825. This is corroborated by a note in Flora (Bot. Zeit.) 1825, Bd II, Beil. 3, p. 33 –35.

In this work a fossil genus *Bucklandia* Presl in Sternb. is described belonging to the Tertiary Cycadaceae, typified by *Clat(h)raria anomala* Mantell as *Bucklandia anomala* (Mantell) Pr. in Sternb. This genus is recognized in reference works up to the present day and several other species have been referred to it.

In 1828 Brongniart had apparently a different opinion about the identity of *Bucklandia anomala*, and reduced it again (Prod. Hist. Vég. Foss.) to *Clathraria* (as *Cl. lyellii* Mantell), at the same time erecting another genus *Bucklandia* (apparently a superfluous name) based on *Conites bucklandi* Sternb. This procedure is of course illegitimate as *Bucklandia* Brongn. is a clear homonym of *Bucklandia* Pr. in Sternb. It is likely that they are synonyms, but this is irrelevant. For the present the main point is that according to the Rules of Botanic Nomenclature it appears that the generic name *Bucklandia* was pre-occupied at the time it was published for the living genus of the Hamamelidaceae. As the latter has no synonyms there seems no other way out than giving it a new name. For this I propose

Symingtonia, in honour of Mr C. F. Symington, late Forest Botanist in the Forest Research Station, Kuala Lumpur, whose lamented death deprived Malaysian botany of one of its prominent students.

The allied genera are, according to Chang (Sunyatsenia 7, 1948, p. 63 seq.) *Mytilaria* and *Chunia;* the latter seems closest allied to *Symingtonia.*

SYMINGTONIA, nom. nov.

Bucklandia R. Br. ex Griff. in As. Res. 19, 1 (1836) p. 94, t. 13—14; non Presl, in Sternb. Tent. Florae Primordialis (1825) p. xxxiii; nec Brongn. Prod. Hist. Vég. Foss. (1828) p. 128.

Symingtonia populnea (R. Br. ex Griff.) comb. nov. - *Bucklandia populnea* R. Br. ex Griff. l.c. — *B. populifolia* Hk. f. & Th. J. Linn. Soc. 2 (1858) 86. — *Liquidambar tricuspis* Miq. Fl. Ind. Bat. 1 (1858) 1097. — *B. tricuspis* Hall. f. Med. Herb. Leiden no. 37 (1918) 14.

The Malaysian specimens differ a little from those of continental Asia in having generally somewhat smaller leaves and narrower, more hairy stipules. However, I cannot find a sharp distinction.

Both in Malaysia and continental SE. Asia *Symingtonia* is growing under the cool hill conditions of the montane zone, 1000—2400 m altitude, from India and Tonkin down to the Malay Peninsula and throughout Sumatra.

Symingtonia tonkinensis (Lecomte) comb.nov. — *Bucklandia tonkinensis* Lecomte, Bull. Mus. Hist. Nat. Paris 30 (1924) 392.

Apparently differing only by the markedly larger fruit and seed. I am not wholly convinced that it deserves specific status.

ON THE EFFICIENCY OF CHLORELLA GROWTH *

BY

B. KOK

T. N. O. Solar Energy Research Project, Laboratory for Plant physiological Research, Agricultural University, Wageningen

(Received June 30, 1952)

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INTRODUCTION**

One of the most intensively studied aspects of photosynthesis is the efficiency of the conversion of light into chemical energy. Under optimal conditions, in steady state experiments of short duration, about 8 quanta are used per molecule of oxygen evolved (1) which means an efficiency of at least 25 % of the light energy when white light is used. There is a striking difference between this efficiency and the efficiency of the photosynthesizable solar radiation observed in agricultural crops which is at most 2 % (2, 3). Until now, the factors responsible for this discrepancy hardly received the attention they certainly deserve. Or, to state it in another way, basic knowledge of plant photosynthesis up to the present, has not been incorporated into agricultural conceptions to the same extent as many other fields of science. This seems to be changing rapidly now. Moreover, it is remarkable that along with these considerations the type organisms of photosynthesis: green algae, are introduced into growth experiments. They are easy to study and to control, show great versatility, and algal cultures are likely to be handled more easily in such a way as to avoid limitations impeding the efficiency of the light conversion in higher plant.

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* Communication No. 99 of the Laboratory of Plant Physiological Research; 32nd Comm. on Photosynthesis. — 30th Comm.: Proc. Kon. Ned. Akad. v. Wet. Amsterdam *C 55*, 34 (1952); 31st Comm. to appear in Carnegie Report on Algal cultures, in press.

** Investigations along the lines of thought pointed out here were initiated by Prof. WASSINK in this laboratory. A research program under his direction is sponsored by the Dutch Organisation for Applied Scientific Research (T. N. O.). The author is much indebted to Prof. WASSINK for many discussions and kind aids.

Aiming at mass-culture of algae as another way for converting solar energy into organic matter, it is clear that the soundest basis for comparison with agriculture is the efficiency of light conversion, $\frac{\text{energy fixed}}{\text{incident energy}} \times 100$. Until now, only quantum yield estimations based upon oxygen evolution in experiments of short duration under laboratory conditions are available and we are in want for an analysis of overall efficiency of green plant growth and its governing factors.

In the experiments, reported in this paper the efficiency of growth of *Chlorella* has been estimated under various conditions. Essentially this has been made by measuring the amount of light absorbed by a culture of algae and estimating the amount of energy fixed in this culture during growth in determining the heat of combustion of the harvested cells. Besides this, the use of large Warburg-manometer vessels as culture flasks made possible continuous checks on the rates of photosynthesis and respiration. In this way a sufficient number of data was obtained for a complete balance of the energy transformations occurring in a suspension of growing algae.

In Chapter I, the experimental procedure is described. Chapter II deals with the efficiencies observed, attention being focussed on the optimal values. Various observations on algal growth in relation to the efficiency are presented in Chapter III.

Chapter I

EXPERIMENTAL PROCEDURE

1. Apparatus

The culture device was a Warburg apparatus. A thermostat (100 × 30 × 25 cm) with a glass bottom and a rigid shaking frame (circular motion 8 mm, 250 rev./min.), was used. A vessel is shown in fig. 1. Its total volume was about 250 ml in which up to 125 ml of suspension could adequately be used with smooth circular shaking. Three ml of diethanol amine solution were applied in the upper

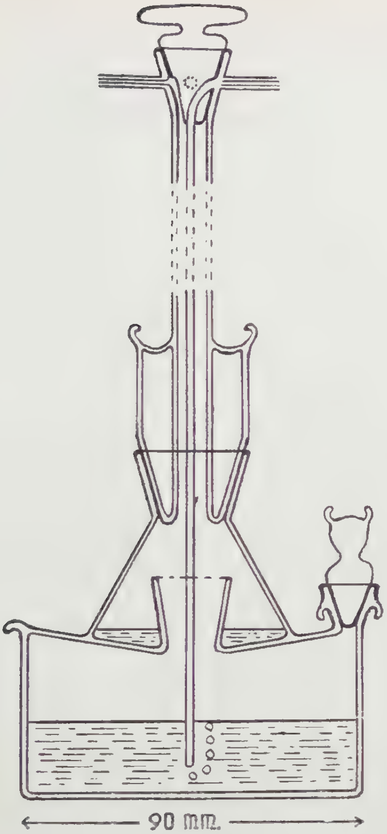
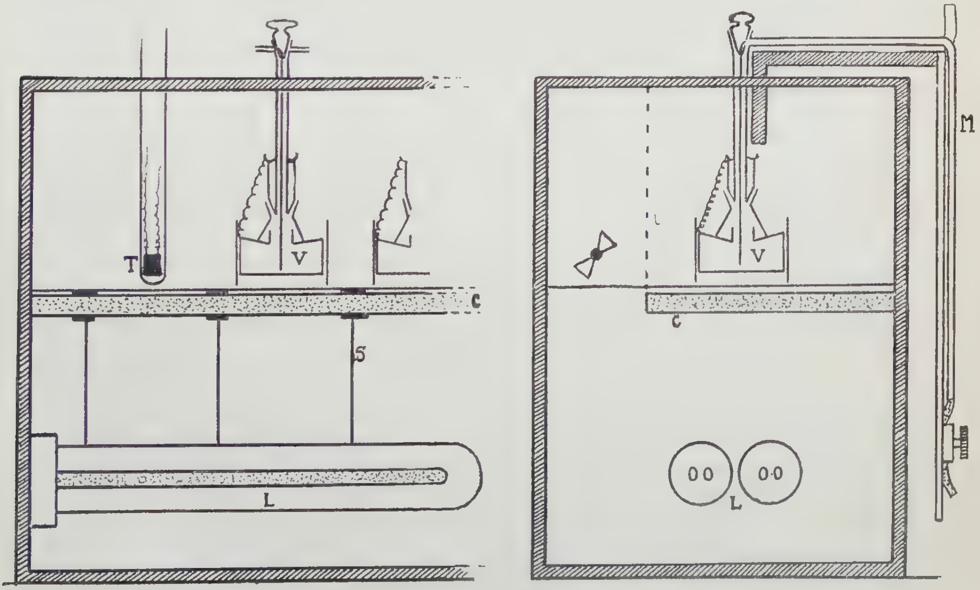


Fig. 1. Type of vessel used. Manometer is attached to stopcock, perpendicular to drawing (dotted circle drawn in the center). Turning the stopcock 90° clockwise closes the gas in- and outlets, and connects vessel to manometer.

Fig. 2. The arrangement for illumination in the thermostat of the manometer vessels containing the algal cultures. L: sodium lamps, S: screens, C: glass box containing copper sulphate solution, V: vessel, T: thermophile, M: manometer.



compartment. A special stopcock was used to allow either saturation of the suspension with gas (air containing 3 % CO_2) or reading of the manometer. The vessels and the manometers were fixed on rigid manometer blocks provided with supporting iron strips. Six manometers and a thermo-barometer of smaller size could be used in the thermostat. A diagram of the set up is shown in fig. 2.

In an experiment, each vessel was surrounded by a blackened metal cylinder extending about 2 cm upwards and downwards, to screen off stray light. The cylinders could be provided with a glass filter to adjust the incident light intensity. Sodium light, filtered through 1 cm 6 % $CuSO_4$ solution was used. The number of lamps and their distance from the reaction vessels could be varied as desired. When all the vessels were illuminated with the highest light intensity used (about 2×10^4 ergs cm^{-2} $sec.^{-1}$), four Philips lamps SO 1000 and one SO 250 had to be used. Small screens and strips were used to restrict obliquely incident light. Though a higher light intensity would be desirable for various studies, this set-up proved to be satisfactory especially with respect to the homogeneity of illumination and the angle of incidence for these large vessels (ϕ 9 cm), and allowed a reliable estimation of the efficiency.

The incident light intensity was measured with an especially adapted thermopile with a large angle of incidence, enclosed in a glass tube with a hemispherical bottom. It could be placed in the thermostat at any place and depth desired.

Light absorption by the contents of the vessels was measured with a large integrating "sphere" (a cube — sides 150 cm — with corners cut off). The construction of the sphere and the measurements were performed according to the principles described earlier. (1). The object-holder was installed in such a way that during the absorption mesurement the vessels could be shaken as in the thermostat.

2. PROCEDURE

Chlorella was cultivated in Erlenmeyer flasks, small glass tubes passing through the cotton plugs, which tubes allow for continuous supply of the cultures with air containing 5 % of carbon dioxide. The cultures were continuously shaken (amplitude 2 cm, 90 times per min.) on a frame (120 × 60 cm) provided with a glass bottom, 12 cm below which a set of 4 fluorescent tubes (2 "day light" and 2 "warm white") burned continuously. The illumination intensity at the bottom of the flasks was ~ 4000 lux.

Only young cultures in pure KNOP solution were used for the experiments. The amount of algae required was centrifuged, and after eventual washing resuspended in fresh culture solution. From this suspension definite amounts were pipetted into the manometer vessels each of which was provided with 3 ml of a 40 % diethanol amine solution (containing 0.1 % thiourea, *cf.* KREBS [4]) in the central compartment. Some samples were placed in the dark at 0° C. A measurement of the light absorption (α) was made. Then, the vessels were fitted to the manometers, placed in the thermostat, shaken, and illuminated. During this period, air with 3 % of carbon dioxide passed through the vessels. Thereafter a measurement of the rate of photosynthesis (P), during 1—2 hours, and subsequently a measurement of dark respiration (R), during the next 1—2 hours, were made. These measurements of α, P, and R were repeated daily whereas in the long intervals illumination and gas supply went on continuously.

After some days, the cells were harvested, washed with distilled water, dried for some hours at 90° C, and finally at 105° C in vacuo. The control samples of cells, stored at 0°C, were treated in the same way. No measurable loss of weight occurred during storage in these samples. For each vessel the difference in dry weight between the experimental culture and the control represented the amount of organic material formed during the experiment. The greater part of the samples collected were analysed for determination of the percentages of C, H, N, and ash[1].

Some experimental details and some additional experiments made in these respects are discussed in the next chapter.

3. On the use of monochromatic light

The use of monochromatic light simplifies or even only enables the accurate estimation of the total amount of absorbed energy. It is possible, however, that cellular processes correlated with growth are selectively influenced by light of some other part of the spectrum than the one used. The following indication was obtained that this was not the case in our experiments. Parallel cultures of *Chlorella* were irradiated during 10 days in various spectral ranges (5) with about the same quantum intensity, representing ~ 1200 ergs cm $^{-2}$ sec.$^{-1}$ for red light. The result is given in fig. 3. Growth rate, measured by cell count and cell volume roughly follows the absorption spectrum of the photosynthetically active pigments. A more detailed analysis of this problem is difficult, owing to changes in the absorption spectrum as the cultures become denser. In another experiment one of the cultures in the Warburg thermostat received a small amount of incandescent light in addition to sodium light during growth. This did not improve the yield in any unexpected way. Thus, there are no indications that the quality of the light that we used was in any way suboptimal.

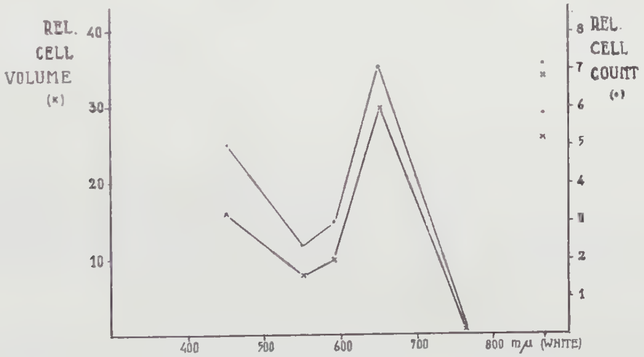


Fig. 3. Growth of dilute *Chlorella* suspensions in various wavelengths. Cell count (.) and cell volume (×) both in relative units.

4. The measurement of gas exchanges

The use of diethanol amine as a CO_2-buffer is advantageous and is allowed since γ (CO_2/O_2) may be computed from the elementary composition of the cellular material formed. The rather low reaction rate between CO_2 and the amine in this set up is of no importance for these long time experiments; constant rates proved to be attained in about one hour. However, in view of the small amount of buffer, which could be used in the vessels described (3 ml of a 40 % solution), corrections were necessary. From the equilibrium data published by MASON and DODGE (6), the curve represented in fig. 4 was computed. In this curve, the amount of CO_2 (P, in μl) evolved or absorbed from 0.012 mol. (3 ml 40 %) diethanol amine for each percent change in CO_2 concentration of the gasphase, is plotted as a function of the initial percentage of CO_2 in the gas phase. In fact this curve holds only for small exchanges.

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[1] Thanks are due to Dr G. J. M. van der Kerk, head of the Dept. of Organic Chemistry T. N. O., Utrecht for carrying out these series of micro-analysis.

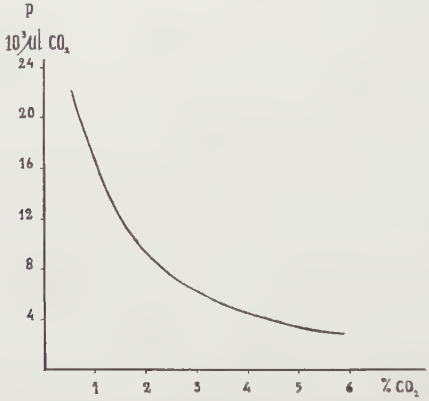


Fig. 4. See text. Data for 25° C.

For each percent decrease in CO_2 tension in the gas phase of a manometer vessel, P μl CO_2 are delivered by the buffer and $0.01\ (V_g + a\ V_f)$ μl CO_2 by the gas and liquid phases. The latter fraction causes a manometer deflection and consequently the readings do not only represent oxygen exchange. Representing the photosynthetic quotient by $\gamma = -CO_2/O_2$, γ μl CO_2 is taken up per μl O_2 evolved. The fraction y originating from the gas phase and suspension liquid of a CO_2-uptake γx amounts to

$$y = \gamma x \frac{0.01\ (V_g + aV_f)}{P + 0.01\ (V_g + aV_f)}\ \mu\text{l}.$$

This amount of gas leads to a manometer deflection:

$$h_{CO_2} = \frac{y}{k_{CO_2}}\ \text{mm}.$$

The resulting manometer reading is: $h_{O_2} - h_{CO_2} = x/k_{O_2} - y/k_{CO_2}$. We now can derive the true O_2 evolution according to the formula:

$$x_{O_2} = h \frac{k_{O_2}}{1 - \dfrac{\gamma\, k_{O_2}}{0.01\, P + k_{CO_2}}}$$

in which, as usually, h represents the observed manometer deflection in mm and k_{O_2} and k_{CO_2} the vessel constants.

Dependent on the composition of the gas mixture used, on the vessel constants and on γ, this correction amounted to 8 – 20 %.

From the elementary composition of the cells, γ could be computed for photosynthesis only; for the corrections of the measured respiration rates, an average value $\gamma = 1.2$ (12) was used.

5. The measurement of the absorbed light

The illumination of the manometer vessels was homogeneous within about 5 %. The mean intensity (I) was obtained by averaging over various areas. The sensitive surface of the thermopile was put at the same height as the bottom of the vessel, so that the intensity of the light entering the vessel was measured. Both in the thermostat and in the sphere the area of the light beam was larger than the area of a vessel.

The daily procedure of absorption measurement was as follows: Galvanometer deflections were read after successively placing the following vessels into the object holder of the sphere: vessels 1 to 6, containing *Chlorella* suspensions (U_1—U_6), another vessel containing water (blank reading U_B) and a "black glass" (zero reading U_Z). In the last measurement, the opening in the objectholder (surface = 66 cm^2) was completely shut off by the glass, so that only stray light was responsible for the galvanometer deflection. From these data, a was computed as $1-\frac{U-U_Z}{U_B-U_Z}$, U being U_1 to U_6 respectively. Incident light intensities were measured in ergs cm^{-2} sec.$^{-1}$. The total amount of light absorbed by the suspension during the time of illumination t (in sec.) was I. a. 66. t ergs. The mean light absorption ($\bar{a}$) and the total oxygen evolution during the whole growth experiment could be computed graphically. In this way the total amount of light, taken up during the growth period, I. $\bar{a}$. 66. t ergs, was found.

From the rates of photosynthesis and respiration, quantum numbers were obtained daily.

6. Estimation of the energy fixed

Micro-elementary analysis was advantageous, since it could be carried out with milligram quantities, and since its results could be used to obtain some insight into the composition of the cells by computation of the relative amounts of protein, carbohydrate and fat. The amount of energy fixed in a sample showing an increase in dry weight of a mg (on an ash free basis) and a composition of c %C, h % H, n % N and o % O was computed as follows: Complete oxidation would use

2.5×10^{-6} a $(0.33c-h-0.125o)$ = M mol. of oxygen;

if per mol. O_2 used, H kcal. are evolved, the material formed represents M × H kcal.

A direct check of this computation appeared to be very important. Therefore, we are much indebted to Prof. Coops (Org. Chem. Lab. V.U. Amsterdam) for carrying out some estimations of the heat of combustion with the bomb calorimeter.

From three parallel samples of dried algal material, either analysed or combusted (a, b, c), the following data were obtained:

a: Elementary composition 50.44 % C, 7.07 % H, 9.58 % N, 8.48 % ash.

b: 4.7 % ash, heat of combustion 5.7924 kcal./gram } mean: 5.77 kcal./gr.
c: 5.5 % ash, ,, ,, ,, 5.7473 kcal./gram

Unfortunately, the ash estimations showed variations. From these data a value of H = 112 kcal./mol. O_2 results for the *Chlorella* samples discussed. This value was generally used in our calculations. Probably, the errors introduced by neglecting the energy content of the ash and those introduced by the artificial drying, are of minor importance. An estimation of the overall accuracy of the final efficiency values is rather difficult, since so many data were to be collected. Generally, a good agreement between duplicates was found and the absolute values reported are likely to be significant well within about 10 %.

Chapter II

STUDIES AIMING AT THE OPTIMUM EFFICIENCY

1. Description of a typical experiment

About 10 experiments lasting 3—8 days, and a few covering shorter periods were made.

Fig. 5*a*—*f* contains data about an experiment with cells of low efficiency. Cells from a 4 days old culture (2.5 μl cells/ml), were resuspended in regular Knop medium so as to yield a cell density in the vessels of 1.5 $\mu l/cm^2$, $\alpha_0 \simeq 0.36$. One vessel was kept in darkness and 4 vessels were illuminated with various light intensities. Fig. 5*a* shows the rate of photosynthesis (P), measured first, and the rate of respiration (R), measured after an illumination period, as ordinates plotted against the amount of light absorbed in each vessel (α I) as abscissae. The straight line indicates equal quantum numbers (ca. 9 quanta/mol. O_2) for all samples. The stimulation of respiration by a few hours illumination is remarkable, and is practically proportional to the intensity. Figs. 5*b*, *c*, *d* show similar observations for the following 3 days. Owing to cell multiplication, α is increased the second day (fig. 5*b*). In the highest light intensities, however, the rate of photosynthesis did not increase proportionally. A further decline in yield and ad ecrease of P/P—R is found the following two days (fig. 5*c*—*d*). Fig. 5*e* shows the increase of α and of the quantum-number and the decrease of P/P –R during the period of exposure, for one vessel. Fig. 5*f* shows the ultimate increase in dry weight of the samples, dependent on the irradiation intensity. The results of two similar experiments are given as dotted curves. Obviously, the experiment discussed led to rather low overall efficiencies, varying from 6 to 11 % fixation of the absorbed light energy.

2. General considerations

The "efficiency" we were aiming at in these experiments needs some further discussion. Most measurements of photosynthetic efficiency have been made manometrically. The results thus obtained, however, only have a definite meaning if the overall reaction occurring in the cellular suspension is well known.

Even in steady state experiments considerable variation in the type of reactions carried out by *Chlorella* cells is possible. For this reason, the measurement of the rate of CO_2 uptake is less desirable and also the determination of O_2 evolution is not completely unambiguous. The following example will demonstrate that only the knowledge of the composition of the material and the conditions under which it is formed allow the computation of definite efficiency values. We can take, *e.g.*, the sample described on page 451, with a molecular composition $C_{6\cdot14}\,H_{10\cdot3}\,O_{2\cdot24}\,N$ ("mol. wt". 134). The formation of this material puring photosynthesis in a NO_3-containing medium can be represented according to equation (1), γ being —0.69.

$6.14\ CO_2 + 4.7\ H_2O + HNO_3 \rightarrow C_{6\cdot14}\,H_{10\cdot3}\,O_{2\cdot24}\,N + 8.9\ O_2$ — 822 kcal. (1).

As far as energy conversion is concerned, essentially the reverse of reaction (1) takes place in the bomb calorimeter. Neglecting the heat content of the ash, we may calculate 822 kcal. ($134 \times 5.77 \times 1.062$) as the amount of energy fixed. Neglecting respiration losses and assuming a quantum number of 8 $h\nu$/mol. O_2, the efficiency of conversion at $\lambda = 6800$ Å would amount to $\frac{822}{8.9 \times 8 \times 41.5} = 27.8\ \%$. In this case, 92.4 kcal. would have been fixed per mol. O_2 evolved in photosynthesis.

In separate experiments (8), we measured equal quantum numbers for O_2 production in media containing either NO_3^- or NH_4^+. Now, if *Chlorella* cells, similar to those discussed above, should have been grown with ammonium as the source of nitrogen, synthesis would have occurred according to equation (2), γ being —0.89, and taking into consideration that reduction of nitrate to ammonia consumes 81 kcal./mol.

$$6.14\ CO_2 + 3.7\ H_2O + NH_3 \rightarrow \rightarrow C_{6\cdot14}\,H_{10\cdot3}\,O_{2\cdot24}\,N + 6.9\ O_2 - 741\ \text{kcal.} \qquad (2)$$

In this case a quantum number 8 would mean an overall yield of $\frac{741}{6.9 \times 8 \times 41.5} = 32.4\ \%$. Per mol. O_2, evolved in photosynthesis, now 107.4 kcal. are fixed, and a 17 % better efficiency is obtained. Apparently, NO_3 reduction in the light runs with a low efficiency $\frac{81}{(8.9 - 6.9) \times 8 \times 41.5} = 12\ \%$. From a merely economical point of view it is of interest that, theoretically, by ammonium feeding higher efficiences than with nitrate might be expected, as much as 30 % $\left(\frac{8.9}{6.9}\right)$ in the case discussed.

3. Results

In Table I, some data of an experiment (no. 7), leading to high yields under various conditions, are collected. 550 μl *Chlorella* cells (our strain A) originating from a 2 days old culture in Knop solution (density 1.5 μl/ml), after washing were resuspended in 210 ml nitrogen-poor medium (C after SPOEHR and MILNER [7], diluted 4 times). From this suspension, an amount of 25 ml, containing 66 μl of cells was pipetted into each vessel, while two samples of 25 ml were stored at 0° C. In vessel no. 4, another 75 ml of the same medium were added, whereas the other vessels each received 75 ml of normal KNOP solution (pH 5.0). All vessels were provided with

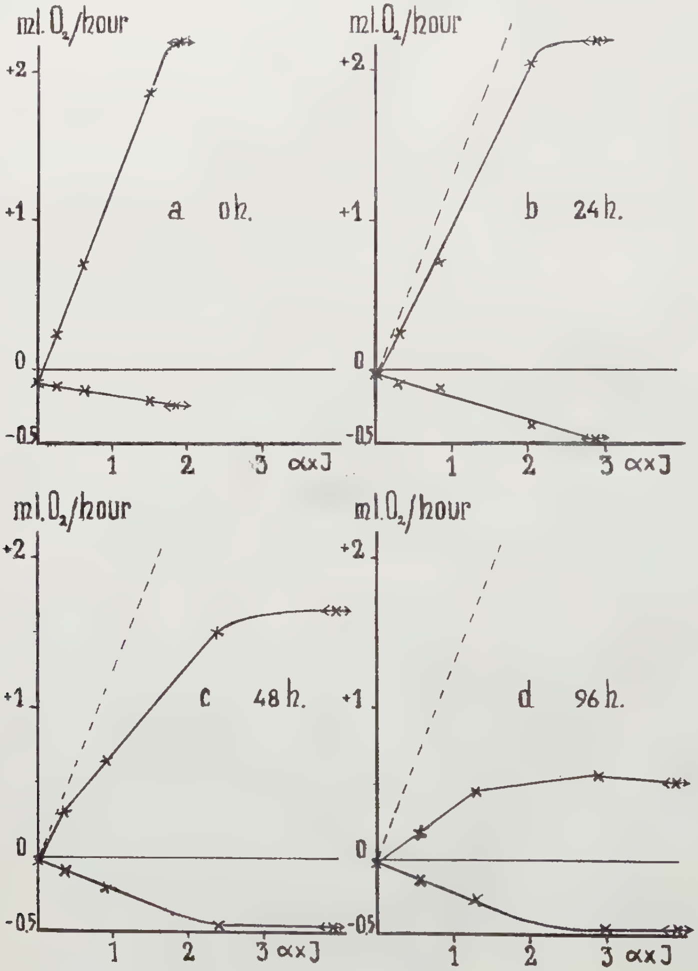


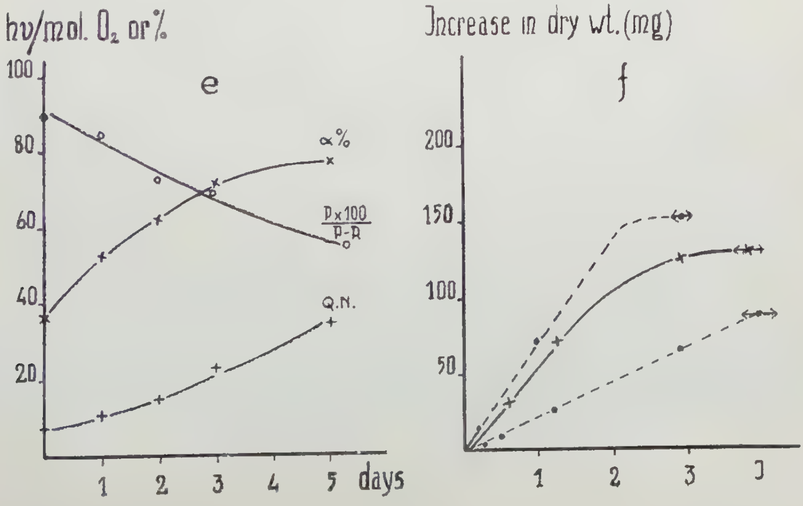
Fig. 5. Exp. No. 4. Photosynthetic and respiratory rates dependent on light intensity and time. The dotted lines in *b*—*d* indicate the initial slope shown in *a*. One vessel (indicated ←×→) was painted white outside in order to increase the mean intensity ← this however prevented accurate estimations of αI. Abcissae in *a*—*d*: αI in relative units, the same for all figures, 1 relative unit is about 17×10^4 erg/sec. Fig. 5*e*: increase in α and quantum number, and decrease of P/P—R × 100 with time, for one vessel; fig. 5*f*: increase in dry weight with light intensity, I in relative units.

TABLE I

The efficiency of light energy conversion and some other data concerning growing cultures of *Chlorella vulgaris*, strain A (Exper. no. 7).

Time hours	Vessel no. . . .	2	3	4	5	6
	Inc. int. ergs cm^{-2} sec.$^{-1}$ $\times$ 10^{-3}	7.9	dark	14.8	17.9	13.3
1–3	Quant. no. . . .	10.1	—	9.0	10.2	9.1
18–21	Quant. no. . . .	8.5	—	11.1	8.7	8.9
	P/P–R	0.94	—	0.94	0.94	0.95
41–44	Quant. no. . . .	8.0	8.1	13.6	—	8.3
	P/P–R	0.95	0.93	0.95	—	0.89
65–68	Quant. no. . . .	7.5	—	19.6	10.2	9.1
90–94	Quant. no. . . .	8.1	10.0	35	—	9.8
	P/P–R	0.92	0.92	0.74	—	0.86
94	α	0.91	0.86	0.51	0.85	0.93
Total time illum. (hours) .		85.5	44.5	85.5	41	85.5
,, ,, darkened (,,) .		8	49	8	52.5	8
Increase in dry weight mg (0° C: 13.3 mg)		101	84	82	82	176
El. analysis % C		48.51	46.90	50.91	48.44	43.53
,, % H		6.93	6.73	7.49	6.75	6.43
,, % N		8.25	9.01	2.43	10.59	5.58
,, % ash.		12.73	13.72	4.64	11.31	14.58
Efficiency (per cent). . . .		23.5	18.6	15.1	20.4	18.2
% protein		58	64	16	71	40
% carbohydrate		19	19	54	8	46
% fat		23	17	30	17	14
Heat of combustion kcal./gr (calculated)		5.75	5.63	5.38	5.76	5.90
γ computed from elementary composition		0.70	0.70	0.78	0.68	0.74

— = dark period (vessel 3 and 5)



3 ml 40 % diethanol amine and flushed with air containing 2.8 % CO_2. The temperature was 25° C, the absorption (a) in sodium light of the various samples at the start was 0.21 to 0.22 of the incident light. One place in the thermostat was darkened, which was used to put the vessels 3 and 5 alternately in dark and light, by mutually interchanging them every 24 hours. As usually, photosynthesis, respiration, and fractional absorption were measured daily, and from these data the quantum number, and P/P—R were calculated.

The final elementary analysis showed the character of the reaction which had actually occurred. Generally, we found very satisfactory agreement between the measured amounts of oxygen evolved and the amounts and compositions of cellular material built up. We will discuss in some detail the results obtained with vessels 2, 4 and 6 from this experiment:

Vessel 2: Elementary composition of the cellular material harvested: $C_{6.85}H_{11.8}O_{2.65}N$ ("mol. wt". 150).
Synthesis occurred according to:

$$6.85\ CO_2 + 6.4\ H_2O + NO_3^- \rightarrow (C_{6.85}H_{11.8}O_{2.65}N + 9.7\ O_2 + OH^- \qquad (3),$$

γ being —0.71. An increase in dry weight of 88 mg ash free was found. This corresponds to an oxygen evolution of:
$\frac{88 \times 10^{-3}}{150} \times 9.7 \times 22.4 \times 10^6 = 12.8 \times 10^4$ mm³ O_2, whereas a total O_2-evolution of 12.3×10^4 mm³ was computed from the daily manometric measurements.

Vessel 4: (low N vessel) Elementary composition: $C_{24.5}H_{43.3}O_{12.5}N$ ("mol. wt." 550).

$$24.5\ CO_2 + 20.2\ H_2O + NH_4^+ \rightarrow (C_{24.5}H_{43.3}O_{12.5}N) + 28.6\ O_2 + H^+ \qquad (4),$$

γ being — 0.86. Increase in ash free dry weight: 78.3 mg.
Corresponding O_2 evolution: 9.13×10^4 mm³.
Actually measured: 9.0×10^4 mm³.

Vessel 6: Elementary composition: $C_{9.15}H_{16.2}O_{4.96}N$ ("mol. wt." 219).

$$9.15\ CO_2 + 8.6\ H_2O + NO_3^- \rightarrow (C_{9.15}H_{16.2}O_{4.96}N) + 11.8\ O_2 + OH^- \qquad (5).$$

γ being — 0.78. Increase in ash free dry weight: 150 mg.
Corresponding O_2 evolution: 18.1×10^4 mm³.
Actually measured: 19.8×10^4 mm³.

In vessel 2, one of the highest efficiencies observed was recorded. In some shorter (24 h.) experiments the same efficiency was found.

Since the elementary composition did not differ much from the standard sample (*cf.* equation (1), and correcting 6 % for the higher ash content) we may calculate the efficiency directly as $\frac{\text{cals fixed}}{\text{cals absorbed}} \times 100$:

$$\frac{0.94 \times 101 \times 10^{-3} \times 5770 \times 100}{0.24 \times 10^{-7} \times 0.61 \times 66 \times 7.9 \times 10^3 \times 85.5 \times 3600} = 23.5\ \%.$$

in which $0.94 \times 101 \times 10^{-3}$ represents the material formed in grams, 5770 the heat content in cal./gram, 0.24×10^{-7} the conversion factor ergs/cals, 0.61 the absorption factor $\bar{a}$, 66 the irradiated surface in the sphere in cm², 7.9×10^3 the light intensity in ergs cm⁻² sec.⁻¹, and 85.5 × 3600 the time of exposure in seconds. Calculation in the usual way, described also on page 451, led to the same result.

The distribution of all efficiencies obtained in our experiments, is given in fig. 6. The large variation shown is not due to experimental errors, but to differences in environmental conditions. Algae different from our strain A generally yielded lower efficiency values. Prolonged exposures, especially in small amounts of suspension medium per vessel (50 ml) and low nitrogen content were mainly responsible for unfavourable efficiency values (*cf.* Chapter III).

The high quantum yields and low respiration losses, shown by our best cultures, indicate that these yields approach closely the optimum for *Chlorella* and probably for all green plants. An additional improvement, theoretically can be expected from the use of ammonium instead of nitrate feeding, but no experimental data are available. Of a merely theoretical interest is the increase in efficiency by about 15 % to be expected if red light instead of sodium light were used. In our procedure, soluble organic material, eventually excreted by the algae into the culture medium was discarded. According to reports from several sides (7,9) 95 –98 % of the organic material formed is retained in the cells and thus only a small error can have been introduced, neglecting the other fraction.

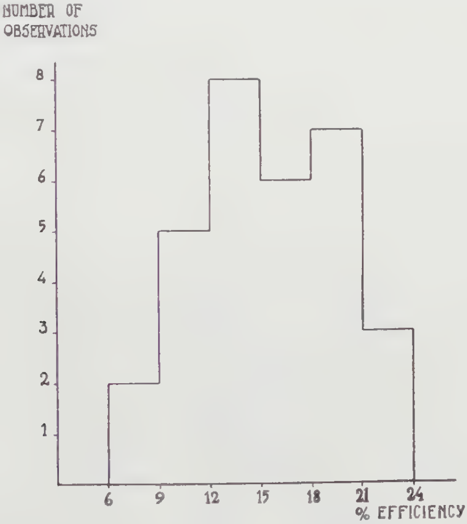


Fig. 6. Distribution of the observed efficiencies.

CHAPTER III

MISCELLANEOUS OBSERVATIONS ON ALGAL GROWTH IN RELATION TO THE EFFICIENCY

1. CHEMICAL COMPOSITION OF THE CELLULAR MATERIAL

Interest was concentrated upon compositions obtained in periods of efficient growth; this mainly restricted the duration of the exposures.

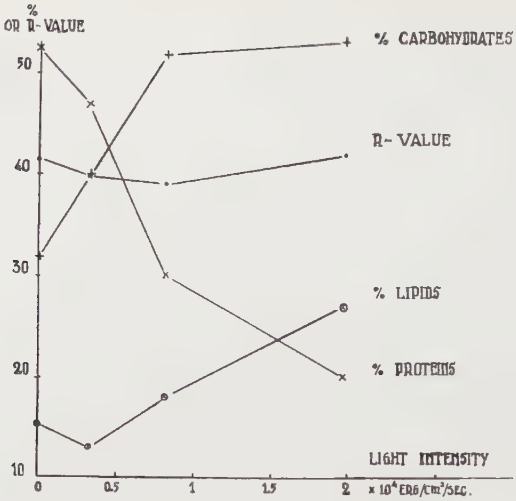


Fig. 7. Influence of intensity of continuous illumination on cellular composition.

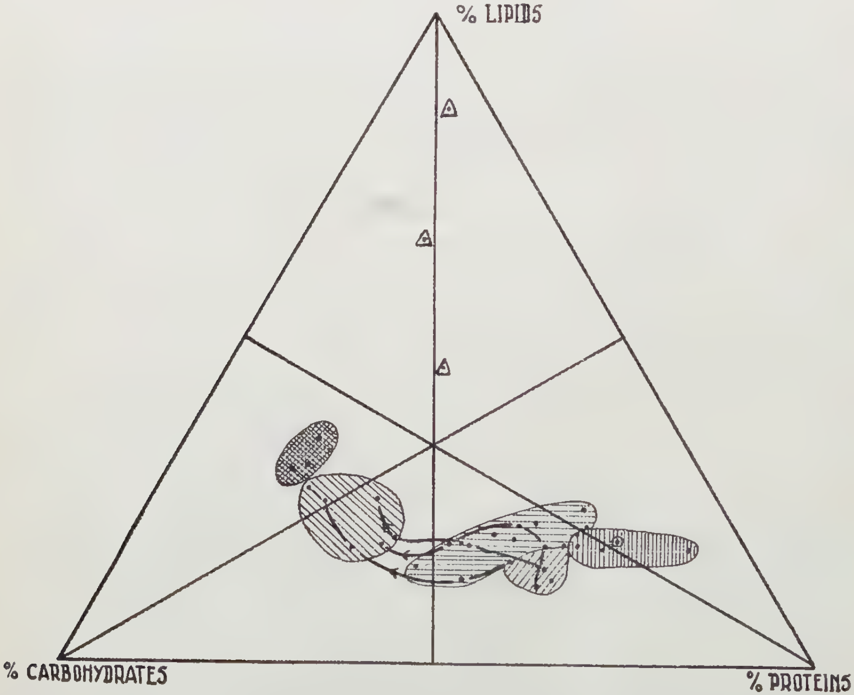


Fig. 8. Chemical compositions found. Data are arbitrarily divided into groups: ▨ dark, ▥ discontinuous illumination with relatively high light intensity (day/night). Other groups continuously illuminated: ▤ low intensity, ▧ high intensity, ▩ high intensity in N-deficient media. Arrows connect data from the same experiment with their points directed towards increasing light intensity. △ Data of SPOEHR and MILNER (7).

40 Analyses, including duplicates, were made. From each analysis, we computed the approximate percentage protein, lipid and carbohydrate, and the heat of combustion per gram (*cf.* Table I). The "R value", introduced by SPOEHR and MILNER (7) theoretically equals 7.6 times the heat of combustion in kcal per gram. For our standard sample we found 7.8.

Some correlations between cellular components and conditions are shown in figs. 7, 8, 9 and 10. Fig. 7 illustrates the effect of light intensity under continuous illumination. As compared to cells kept in the dark, illuminated cells show a decreased protein content, while percentage carbohydrate, and in strong light percentage fat are increased. Three experiments of this type were made. In fig. 8, 9 and 10 the samples of each of these experiments are interconnected by arrows, pointing to increase of light intensity. Moreover, in the figures all points originating from samples with about the same pretreatment are enclosed in "islands" (*cf.* the legend of fig. 8). The effects, shown in fig. 7, are generally found; prolonged continuous illumination and deprival of nitrogen lead to a low protein content, discontinuous illumination induces a high one. Fig. 9 illustrates a correlation between nitrogen and ash content, both being highest in cells grown during day and night cycles, and lowest in nitrogen deficient cells. Small (about 20 %), but rather systematic variations

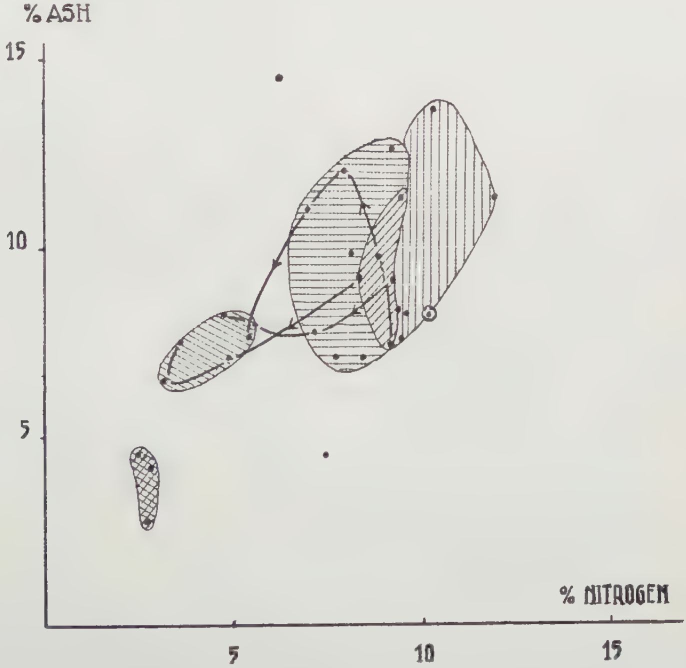


Fig. 9. Relation between ash and nitrogen content. Groups and arrows: the same meaning as in fig. 8.

of the R value were found, the lowest values naturally occurring in carbohydrate rich cells (fig. 10).

The two extreme types may be discussed in some more detail:

1. Cells deprived of nitrogen

In relation to Spoehr and Milner's report on *Chlorella* cells with extremely high lipid content (some of their data are plotted in fig. 8), we tried to follow the growth efficiency of nitrogen deprived cells. Actually, in our definite experiments, we tried to transform normal cells into "fat" cells by transferring an amount of cells, previously grown in Knop medium, into a nitrogen deficient one, in rather dense suspension.

Table I, vessel 4, shows a quick decrease in efficiency. In a dense suspension, the rate of photosynthesis declines with time in both normal Knop medium and in a nitrogen deficient medium, as is shown in fig. 11. Refreshment of the medium, however, did not restore the initial rate in a nitrogen deficient medium as it did with cells normally grown. Smaller and more stable rates of O_2 uptake in the dark are shown in a nitrogen deficient medium. Preliminary observations did not reveal significant differences between the effect of continuous or discontinuous illumination of nitrogen deficient cultures.

Extremely high lipid and low N contents probably are not con-

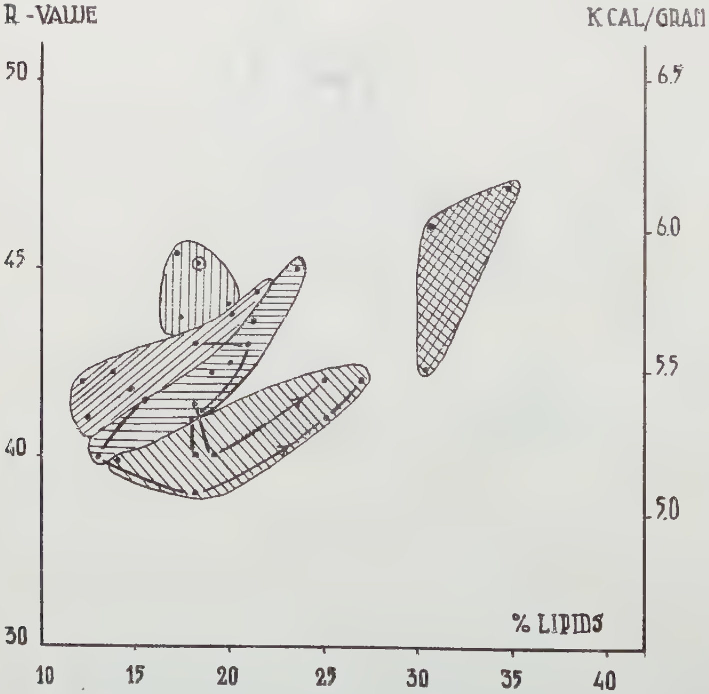


Fig. 10. Relation between R value, heat of combustion per gram and % lipids. Groups and arrows have the same meaning as in fig. 8.

sistent with favourable yields. However, the possibility is not excluded, that a short exposure in nitrogen free medium, following growth in a nitrogen containing one, leads to an optimum compromise.

2. Cells grown in discontinuous light

A considerable and more or less unexpected influence of dark periods upon cellular composition was found. In one experiment daily dark periods of 5 hours were intercalated, in order to follow the decrease of respiration after intense photosynthesis. Even these very short "nights" led to high-protein cells in nitrogen containing media. Cells grown outdoors and exposed to sunlight intensity and natural nights, showed high protein content too [1].

Based on the above and other observations (*e.g.* MYERS and CRAMER [10]), we might propose the following picture. At high

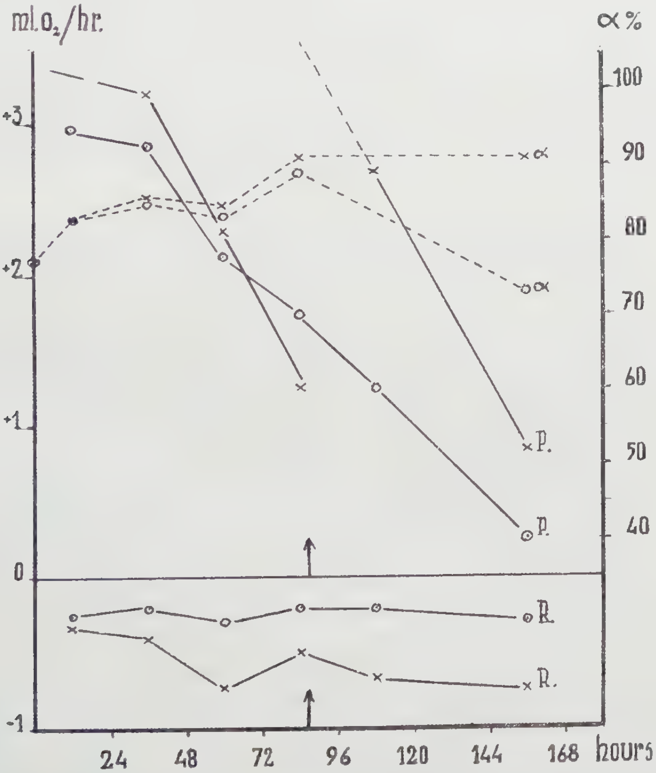


Fig. 11. Exp. 9. Drop of rates of photosynthesis with time. Crosses indicate values for cells growing in KNOP solution. Circles indicate values for a parallel culture in N-deficient medium. Arrows indicate resuspension of both cultures in fresh medium: only in the presence of nitrate the original rate is restored.

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[1] In the summer of 1950 preliminary growth experiments in outdoor tanks (content 150—200 l, irradiated surface 1 m^2) were made. Efficiencies observed did not surpass 2 % utilization of sunlight. This work has been continued during the summer of 1951 by VAN OORSCHOT (*cf.* 16).

light intensities, carbon fixation outranges nitrogen fixation, and cellular composition shifts to low protein content. After prolonged exposures cell division rate and photosynthetic efficiency may decrease. Upon darkening, during the phase of high respiration rate, protein synthesis and cell division restore cellular composition and size. Probably, natural days and nights are of primary importance for the efficient utilisation of bright light, *e.g.*, sunlight.

2. ASSIMILATION AND DISSIMILATION, INFLUENCE OF DARK PERIODS ON THE EFFICIENCY

The respiration of algae in the dark results in a decrease in organic material. During illumination, the fraction of the light used for compensating respiration does not contribute to the formation of new material. Some remarks about both aspects may be made.

1. Respiration losses during illumination

At present, the best index obtainable for the dissimilation rate during illumination is the rate of O_2 uptake (R), immediately after darkening. If the rate of O_2 evolution in the light is P, we obtain (P—R) for the total light action, and the fraction P/P—R results in growth.

Actually, the light may be used twice as efficient for compensation of respiration (4 quanta process) as for oxygen evolution (8 quanta process) in which case the fraction of the absorbed light available for growth would be P/P—0.5 R.

Over a certain range of light intensities, we found a rough proportionality between P and R (*cf.* fig. 5*a*) and, thus, P/P—R constant and characteristic for the set of conditions and the algal material used. Optimal values were as high as 0.95, whereas under bad conditions values as low as 0.3 were observed.

The respiration rate, corresponding to a certain value of P (or of incident light intensity), reaches its final level rather slowly. Apparently this takes 2—3 hours. Exposures of 20—30 minutes to higher light intensities had only small effects upon after-respiration. The decay of R after darkening, discussed more in detail below, even is much slower. Therefore, these effects can be studied adequately only in long lasting experiments.

In fig. 12 the relation between respiration rate and incident light intensity is plotted after exposures of 0, 3, and 95 hours respectively. The rate at the beginning of the experiment ($t = 0$) is determined by the pretreatment of the algae. After 3 hours in dark and at low light intensity, the rate has decreased, whereas it has increased at high intensities. At the end of the experiment ($t = 95$h), respiration in dark was very low, but in strong light too the rate per unit cells had decreased. It was possible to estimate roughly from the course of the light absorption how the mean light intensity per cell: I mean (proportional to $\alpha I/C$, $C =$ concentration at time 0) in the various vessels had changed, owing to the increase in concentration. Plotting the rates against I mean, instead of against the incident intensity, closer agreement between initial and final rates is found. This might constitute an argument for the statement that it is the mean light intensity in a cell suspension which actually determines the respiration rate. An interesting phenomenon is shown by the weakly illuminated suspension. At the start of the experiment, even after 3 hours illumination, respiration was not compensated; after an adaptation period, positive pressure changes in the light and increase in dry weight occurred. A remarkably low respiration, probably representing the endogenous rate, was finally found.

2. Respiration losses during the night

The rate of O_2 uptake after a period of illumination declines slowly, until after about 20 hours a low and steady level of endogenous respiration is obtained (at 25° C we found a rate of about 1 μl O_2/hour/mg dry wt.). This decline was studied by various authors in algae (11, 12) and leaves (13). In fig. 13 some data are collected and plotted as % loss in dry weight versus time. The first steep slope of the curves is correlated with the previous illumination intensity

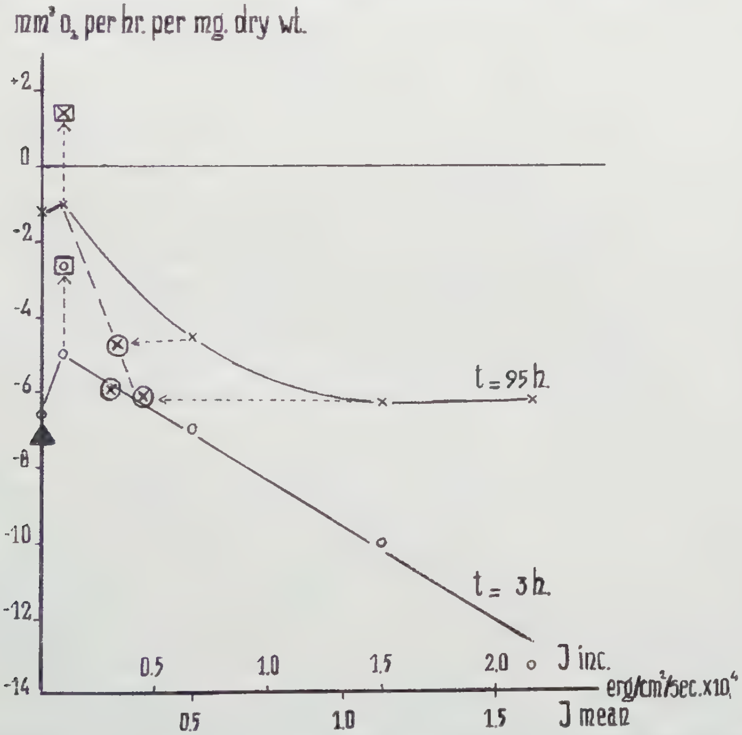

Fig. 12. Exp. 3. Relation between after-respiration and illumination intensity at the start (o) and the end (×) of a growth experiment. After applying a correction factor for the decrease of the mean intensity per cell during growth for the three strongly illuminated vessels, curve —⊗— is obtained for $t = 95$ hours. For the sample with the weakest illumination the initial and final rates of gas exchange in the light are indicated in squares. ▲ : respiration at $t = 0$ hours.

(*cf.* the previous section). So a loss as high as 10 % of the total dry weight during one night at 25° C may correspond to rates of photosynthesis, *e.g.*, doubling the dry weight during day time. In dense suspensions the relative changes probably are much smaller. The net result of natural dark periods thus may be a relatively small decrease (about 10 %) in overall efficiency of light utilisation. Very likely, the effect of these small losses during night periods is many times overcompensated by the benificial effects of the "rebalancing" of the chemical composition of the cells in the dark.

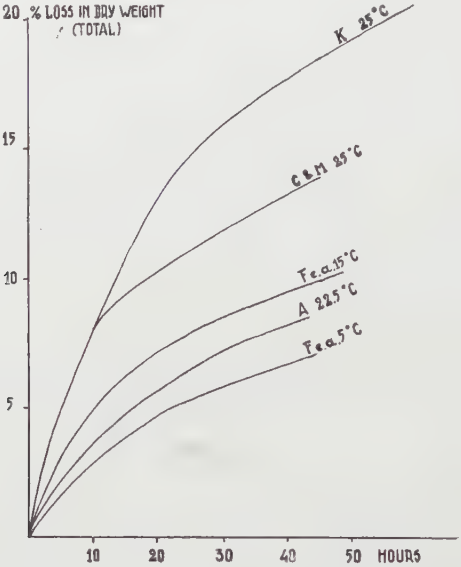

Fig. 13. Percentage loss in dry weight in the dark with time. Data for *Chlorella* after French *et al.* (F.e.a.) for 5° and 15° C, after Cramer and Myers (C & M) and from the present study (K) for 25° C. Data from Audus (A) are for Cherry Laurel leaves (22.5° C).

3. Influence of light intensity and time

In the experiments in which various light intensities were applied, a linear relation between increase in dry weight and intensity was observed. Under constant illumination intensity, proportionality between dry weight and time of exposure was found. The linear relation between growth and I t, in fact indicates that the yield is independent of cellular concentration over a range of considerable extension.

Growth of an algal culture in a limited space can be described as follows: Accepting the efficiency of light conversion constant (K_1) and the respiration rate proportional to the concentration (C) of cells K_2C, growth occurs according to:
$dC/dt = \alpha I_0K_1 - K_2C$, $\alpha = 1 - e^{-\beta C}$, in which: I_0 = incident intensity, α = fractional absorption, β = constant.

Substituting: $y = \beta C$, $x = I_0K_1 t$ and $z = K_2/I_0K_1$ (so $z < K_2$ and constant), we get: $dy/dx = 1 - e^{-y} - zy$. At the beginning of an experiment, when a small inoculum is used, $zy \ll 1$ so that $dy/dx = 1 - e^{-y}$, and an exponential growth curve is obtained. When y increases, $e^{-y} \rightarrow 0$ and $dy/dx = 1 - zy$. Upon integration we find for $x \rightarrow \infty$, $y = 1/z$ and $I_0K_1 = K_2C$. This means that ultimately a stationary phase is reached, in which the (totally absorbed) incident light just serves to compensate respiration. Between the initial and final parts of the growth curve a zone occurs in which a nearly linear relation between C and I t exists. The maximum growth rate occurs in this zone at the inflection point of the curve, where the light absorption approaches 100 %. In fact, linear growth occurs over a far more extended range beyond the point of complete absorption than predicted by the foregoing formulae. The decrease of K_2 with time can be held mainly responsible for this.

As described in section 2, the respiration rate per unit cells, instead of being constant, appears to depend on the illumination intensity. When a suspension becomes denser, the mean intensity I_m per cell decreases, resulting in a lower value of K_2. The intensity I_m being inversely proportional to C, over a certain range K_2C might be constant and proportional to I_0, so that $K_2C = K_3I_0$. In this range, linear growth occurs according to $dC/dt = I_0\ (K_1 - K_3)$. Ultimately, however, when the respiration rate approaches the endogenous level, an endpoint of growth is to be expected. Changes in chlorophyll content per cell (influencing β) and in photosynthetic efficiency (K_1), both especially important in strong light cultures, will complicate the picture. In our experiments on the relation between growth and I t, severe difficulties were encountered owing to deterioration of the medium. Increase in cellular concentration (to 2—4 g dr. wt./l) was accompanied by decrease in efficiency. Resuspension of the cells in fresh culture medium only temporarily restored the optimal efficiency (*cf.* fig. 11). Depletion of nitrogen or other major salt constituents of the medium by the cells did not occur. So, probably, either deficiency of micronutrients or auto-antibiosis phenomena have to be considered responsible for the mentioned effects. Recently, by adequate provision of micronutrients, MYERS (14) achieved linear growth of *Chlorella* up to very high densities.

DISCUSSION

Sodium light rather closely matches the mean of the visible solar radiation spectrum and has been found to be converted to cellular material with an efficiency of 15—20 %. Therefore, cultures of algae sufficiently dense to perform complete light absorption, may be expected to convert about 20 % of the incident solar radiation below 7000 Å into cellular material. This efficiency value should be considered as close to the maximum obtainable and more or less as a goal to strive after in mass culturing of algae. Dependent on geographical latitude, this figure would lead to harvests of 100—300 tons dry material per year per hectare. We may put the question in how far there is any hope of practical approach to this efficiency.

The finding of suboptimal values in many cases even though all our experiments were made at non saturation intensities, illustrates the difficulties to maintain optimal conditions for the plant material. No fundamental limitations, however, seem to be involved here. On the other hand, the efficiency values were consistently higher than the ones found until now with algal cultures under natural conditions (16). This strongly indicates that in those cases an additional impeding factor enters the picture: the high intensity of solar radiation, surpassing factorfold the saturation intensity of photosynthesis, even under abundant supply of carbon dioxide (*cf.* also [2]). Experiments with flashing light, now under way, indicate that this limitation neither is a fundamental one (15). But it looks as if there is a long way between the fundamental possibility and its practical and economical realization.

SUMMARY

The efficiency of conversion of light into organic matter by cultures of growing *Chlorella* cells was measured under various conditions. During growth periods of 24—180 hours, we daily measured the incident light intensity, the fractional absorption, and the photosynthetic and respiratory rates. Finally, the increase in dry weight and the chemical composition of the harvested algae were determined. A correlation between chemical composition and heat of combustion was established. In this way a complete balance of the energy transformations during algal growth was obtained.

Efficiencies were expressed as $\frac{\text{calories fixed in organic matter}}{\text{calories light absorbed}} \times 100.$ Optimal efficiencies of 20—24 % for conversion of sodium light, representing about the mean of the visible solar radiation spectrum, were found in culture media, containing nitrate. Under conditions of nitrogen starvation which leads to cells of low protein and high carbohydrate and fat content, the yield dropped rather quickly.

Strong continuous illumination induced cells with low nitrogen-content, whereas cycles of light and darkness favoured the occurence of algae rich in protein. A relatively small decrease in overall efficiency is caused by natural day and night periods. The linear relation found between growth and intensity and time of exposure, which means that the yield is independent of cellular concentration, is discussed.

REFERENCES

1. Kok, B., Enzymologia *13*, 1, (1948).
2. Wassink, E. C., Med. Dir. Tuinbouw *11*, 503 (1948).
3. Spoehr, H. A., Proc. Am. Phil. Soc. *95*, 62 (1951).
4. Krebs, H. A., Bioch. J. *48*, 349 (1951).
5. Wassink, E. C. and C. v. d. Scheer, Proc. Kon. Ned. Akad. v. Wetensch. Amsterdam, *53*, 1064 (1950).
6. Mason, J. W. and B. F. Dodge, Trans. Am. Inst. Chem. Eng. 32—27 (1936).

7. Spoehr, H. A. and H. W. Milner, Plant Physiol. *24*, 120 (1949).
8. Kok, B., in preparation.
9. Myers, J. and J. A. Johnston, Plant Physiol. *24*, 111 (1949).
10. Myers, J. and M. Cramer, J. Gen. Physiol. *32*, 103 (1948).
11. French, C. S., H. J. Kohn, P. S. Tang, J. Gen. Physiol. *18*, 193 (1934).
12. Cramer, M. and J. Myers, Plant Physiol. *24*, 255 (1949).
13. Audus, L. J. Ann. Bot. N. S. *9*, 165 (1947).
14. Myers, J. Unpublished.
15. Unpublished work at Stanford and Wageningen *cf.* note on page 15.
16. Wassink, E. C., B. Kok and J. L. P. van Oorschot: On the yield of light energy conversion in *Chlorella* cultures as compared with higher plants. Carnegie publication (1952, in press).

NOTES ON MALAYSIAN GRASSES II*

BY

P. JANSEN (Amsterdam)

(*Received June 30th 1952*)

DEYEUXIA Clar. ex Beauv.

This genus is closely related to *Calamagrostis* Adans.. Confusion between the two genera in the past was due to the attempt to apply artificial characters in delineating them, e.g. the degree of prolongation of the rhachilla. The unsatisfactory nature of these characters has been emphasized by J. D. HOOKER (Fl. Br. Ind. *7* : 265. 1896).

Miss J. W. VICKERY (Contr. N. S. Wales Nat. Herb. *I*, *2* : 46. 1940) was the first to study the character of the lemma, which is indurate and more or less densely scabrous in *Deyeuxia*, very thin and hyaline in *Calamagrostis*. Besides, the species of *Calamagrostis* have very long, narrow, acuminate glumes with a relatively short lemma and the hairs of the callus usually much exceed the lemma. The species of *Deyeuxia* have relatively shorter and broader glumes, less clearly exceeding or even distinctly shorter than the lemma; the callus hairs are much shorter than or rarely as long as the lemma. With one exception the species of *Calamagrostis* occur on the northern hemisphere, while those of *Deyeuxia* occur in both hemispheres.

The Malaysian species, up till now arranged in *Calamagrostis*, should be transferred without exception to the genus *Deyeuxia*.

1. **Deyeuxia brassii** (Hitchc.) Jansen, nov. comb.

Calamagrostis brassii Hitchc. Brittonia *2* : 116. 1936; Reeder, J. Arn. Arb. *31* : 322. 1950.

Distr. Only known from New Guinea: Mt. Albert Edward (Brass 4205, typus); Mt. Wilhelmina (Brass & Meijer Drees 9711, 9927, 10213); Mt. Sarawaket (Clemens 10238).

The specimens from Mt. Sarawaket differ from the type-specimen in the tip of the lemma, which is longer 4-toothed, the sharp teeth being c. 1 mm long; glumes punctulate-scaberulous with a strongly scabrous nerve; panicle and sheaths purplish.

2. **Deyeuxia sclerophylla** Stapf, Kew Bull. 115. 1899; in Hook. Icon. Pl. t. 2605. 1899.

Calamagrostis sclerophylla (Stapf) Hitchc. Brittonia *2* : 117. 1936.

Distr. Only known from New Guinea: Mt. Scratchley (Guilianetti), 3600 m altitude.

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*) The first part is in print in Reinwardtia vol 2. and will probably appear end 1952.

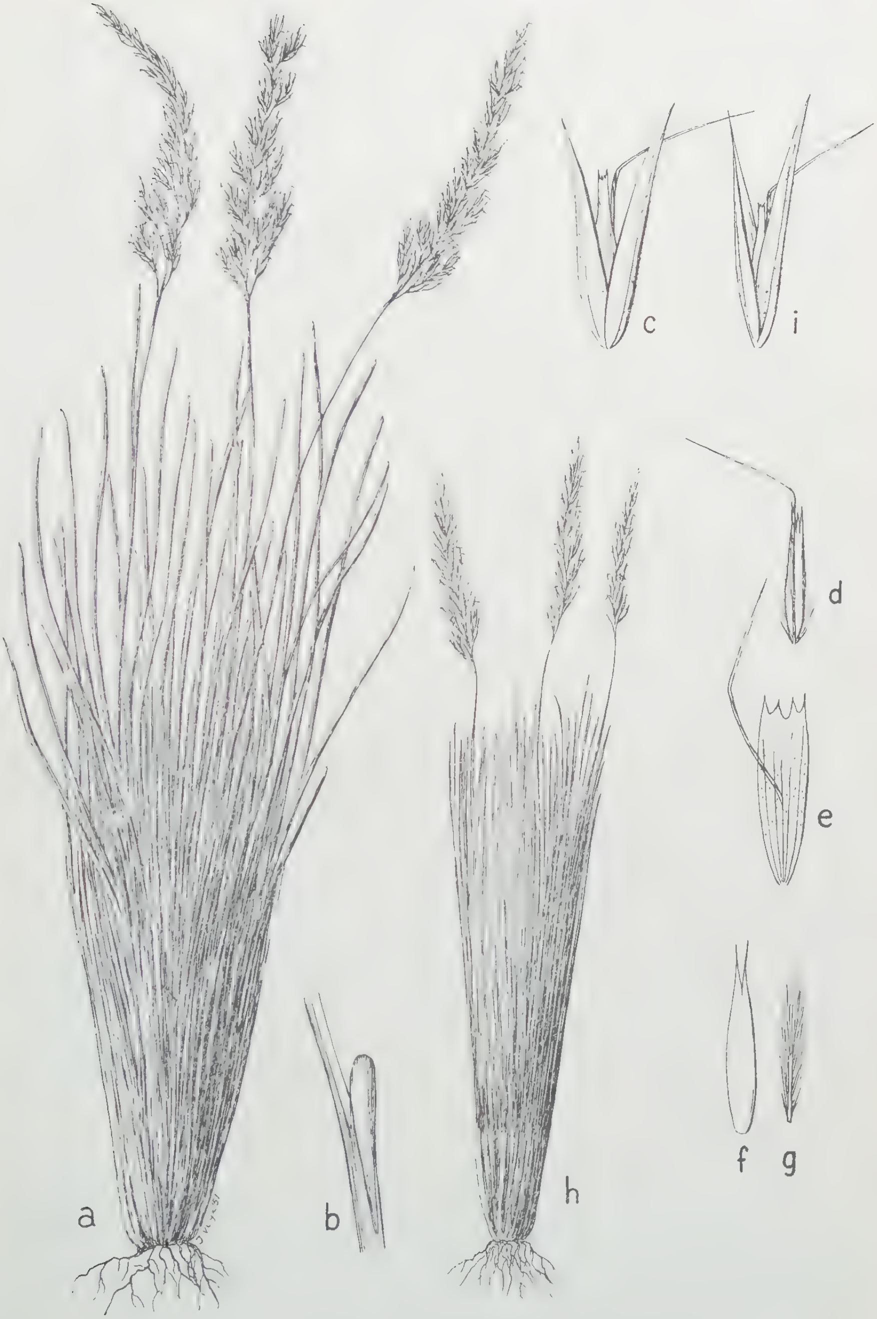


Fig. 1. Deyeuxia macgregorii. *a.* type from Owen Stanley Range. *b.* ligule. *c.* spikelet. *d.* floret. *e.* lemma. *f.* palea. *g.* prolongation of the rhachilla. *h.* specimen from Mt. Knutsford. *i.* spikelet of that specimen.

3. **Deyeuxia macgregorii** Jansen, nov. spec.

Gramen perenne, dense caespitosum. Culmi erecti, paucis nodis, 30—50 cm alti, glabri et laeves vel leviter scaberuli infra tamen proxima paniculam; nodi glabri. Vaginae implerisque ad basin culmorum, internodia superantes, inferiores desintegrantes fibrosae, superiores angustae. Ligula hyalina, 2—2,5 mm longa, obtusa. Laminae anguste lineares, acutae, glabrae, nervis densibus fortibusque, leviter scabrae superne, rigidae, inferiore involutae vel convolutae, usque ad 30 cm longae, superiores breviores et saepe latiores, acutissimae. Panicula breve exserta, laxe contracta, 8—12 cm longa, densior. Axis laevis vel delicate scaberulus. Rami suberecti vel adpressi, raro patentiores in paniculis maturis, inferiores 3—4-nati et 3—4 cm longi, per partem basalem nudi, superiores 2-nati vel solitarii, gradatim breviores, spiculas agentes fere ab insertione. Pedicelli implerisque breviores quam spiculas, delicate scaberuli et paullo incrassati apicem versus. Spiculae 7—8 mm longae, lateraliter compressae, atrovirides. Gluma inferior spiculam aequans, superior paullo brevior, 1- vel sub-3-nervata, scabra imprimis nervo medio et apice versus, lanceolata et acuta. Lemma manifeste brevior quam glumas, 5—5,5 mm longum, scaberulum, 5-nervatum, 2-4-dentatum, aristam dorsalem infra et proxime medium agentem; arista spiculam superat, usque ad 8 mm longa, manifeste geniculata et leviter torta parte inferiore. Palea brevior quam lemma, magis minusve bifida. Antherae 1,5—2 mm longae, latiores. Callus barbatus pilis $^1/_2$ mm longis. Rhachilla ad setam longiorem producta, pilos delicatos agens.

Distr. New Guinea: Papua, near the summit of Owen Stanley Range (MacGregor sin.num., a. 1889, typus in Herb. Melbourne); Mt Knutsford (MacGregor sin.num., a. 1889, in Herb. Melbourne).

The latter specimens are lower with shorter, narrower panicles and slightly smaller spikelets.

Note. The loosely contracted inflorescence resembles that of *Deyeuxia monticola* (R. & Sch.) Vickery (Contr. N. S. Wales Nat. Herb. *1*, *2* : 56. 1941). *D. macgregorii* differs from that species in the awn, which is inserted near the centre of the lemma (and not down to the base), the lemma which is much shorter than the glumes (and not equalling the lower glume), the very scabrous and much longer glumes. In the latter character it would agree with *D. monticola* var. *valida* Vickery (l.c. 57), but the other cited characters distinguish it from this variety.

4. **Deyeuxia atjehensis** (Ohwi) Jansen, nov. comb.

Calamagrostis atjehensis Ohwi Bull. Tokyo Sc. Mus. *18* : 13. 1947.

Distr. North Sumatra: Atjeh, Mts Losir, Goh Lembuh, and Kemiri (Van Steenis 9583, typus, 8371, 8469, 8480, 8593, 9043, 9083a).

Ecol. Locally abundant on slopes and tablelands at 2400—3300 m altitude, in burned scrub or on open soil, not forming a closed stand.

5. **Deyeuxia arundinacea** (L.) Jansen, nov. comb.

Agrostis arundinacea L. Sp. Pl. 61. 1753. — *Calamagrostis arundinacea* (L.) Roth, Tent. Fl. Germ. *2*, *1* : 89. 1789; incl. var. *nipponica* Hack.

Bull. Herb. Boiss. *7* : 652. 1889; incl. var. *brachytricha* Hack. l.c.; Ohwi, Act. Phytotax. et Geobot. *5* : 241. 1936.

When wanting to transfer the name *Calamagrostis arundinacea* (L.) Roth into the genus *Deyeuxia*, we find in Ind. Kew. *1*, p. 74: "*Deyeuxia arundinacea* Beauv. Agrostogr. 160. 1812". This record needs some discussion.

Beauvois described in his work the genus *Deyeuxia* on p. 43 following a manuscript name of Clarion. He cites 4 species "*Arundo Sedenensis, acutiflora* Willd., *Airoides* Mich., *montana* Gaud." They represent respectively: *Deyeuxia varia* (Schrad.) Kunth. 1829; a hybrid between *Calamagrostis epigeios* and *Calamagrostis arundinacea* Roth; *Trisetum melicoides* (Michx.) Scribner; *Deyeuxia varia* (Schrad.) Kunth. 1829.

On this page of the Agrostographie no reference is made to *Deyeuxia arundinacea*. We only find this name on p. 160 in the "Explication des planches et des figures". Here *Beauvois* certainly made an error, as "*Deyeuxia arundinacea*" of Pl. XV fig. XI does not represent a *Deyeuxia*, but the grass that is usually called *Ampelodesmos tenax* Link Hort. Berol. *1* : 136. 1827. This is evident when we look at p. 77 of the Agrostographie. There Beauvois described the genus *Arundo* and cited Pl. XV fig. XI as an illustration of this genus. On p. 78 he proposed the name *Ampelodesma* as a subgenus and ascribed the details of fig. XI to it. Hence "*Deyeuxia arundinacea* Beauv". is manifestly without status, and, hence, a nomen nudum. Therefore the combination *Deyeuxia arundinacea* is not pre-empted.

Deyeuxia arundinacea (L.) Jansen is a species with a wide distribution in Europe and Asia, extending into Malaysia in the mountains of the Philippines (Luzon, Mindanao).

The Philippine specimens are rather variable. The blades of the innovations are more or less complicate to involute, the culmblades are usually flat; the blades are much narrower than in the average European specimens. The panicle is always contracted when young, but some specimens have the short-branched panicle also contracted at maturity (e. g. B. S. 4487). Other specimens have open spreading panicles with long capillary flexuous branches (e. g. B. S. 40222) and there are many intermediate specimens. The spikelets are usually slightly shorter than in the European plants, but they show the same characteristics: palea as long as the lemma, both shorter than the glumes, basal awn tightly twisted below the knee and about twice as long as the spikelet, callus-hairs short.

Merrill referred the Philippine specimens to var. *nipponica* Hack. l.c. (En. Philip. Fl. Pl. *1* : 41. 1923). Ohwi (l.c.) referred other specimens to var. *brachytricha* (Steud.) Hack.

There are specimens more or less agreeing with the description of the first variety, and others with that of the second, but there are more intermediate states. The inconstancy of the panicle-shape is so evident, that it does not seem worthwhile to distinguish these varieties in Malaysian specimens.

6. **Deyeuxia stenophylla** Jansen, nom. nov.

Calamagrostis filifolia Merr. Philip. J. Sc. *1*, Suppl.: 179. 1906; En. Philip. Fl. Pl. *1* : 82. 1923; Hitchc. Brittonia *2* : 117. 1936; Reeder, J. Arn. Arb. *31* : 322. 1950, non *Deyeuxia filifolia* Wedd.

WEDDELL, Bull. Soc. Bot. Fr. *22* : 173. 1875 gave a latin key to the species of *Deyeuxia* from the Cordilleras de los Andes. On p. 178 & 179 he mentioned *Deyeuxia filifolia.*

PILGER, Engl. Bot. Jahrb. 42 : 67. 1908 changed that name into *Calamagrostis filifolia,* overlooking a name already occupied by MERRILL for a Philippine species. HENRARD in Meded. 's Rijksherbarium Leiden 40 : 23. 1921 made the same transfer for the second time.

Distr. Philippines and New Guinea.

Note. Merrill 4537 & 4715 are cleistogamous forms, differing in having 0,5 mm long anthers, persisting with the ripening fruit within the closed glumes.

7. **Deyeuxia australis** (Zoll. & Mor.) Jansen, nov. comb.

Lasiagrostis australis Zoll. & Mor., Mor Syst. Verz. 100. 1846. — *Stipa australis* (Zoll. & Mor.) Steud., Zoll. Syst. Verz. 55. 1854; Syn. 1 : 132. 1854. — *Calamagrostis australis* (Zoll. & Mor.) Buse, Pl. Jungh. 343. 1854; Miq. Fl. Ind. Bat. *3* : 379. 1857; Back., Handb. Fl. Java *2* : 210. 1928. — *Calamagrostis javanica* Steud., Syn. 1 : 194. 1854; Miq., Fl. Ind. Bat. *3* : 379. 1857. — *Deyeuxia javanica* (Steud.) Boerlage, Ann. Jard. Bot. Buitenz. *8* : 71. 1889.

A rather variable species. Usually the spikelets are 5 mm long, but in some specimens from Sumatra they reach 6 mm. The length of the hairs on the nerves of the glumes varies: from minute to 0,6 mm long.

var. *montana*, nov. var.

Culmi geniculatim ascendentes patenteque, 20—30 cm alti. Folia brevia, angustissima, convoluta. Paniculae breves, laxe spicatae. Spiculae distincte breviores, 3—$3^1/_2$ mm longae. Arista 15 mm longa.

Distr. Java: on the windswept mountaintops of Mt Gedeh (Kuhl & v. Hasselt sin. num. in Herb. Bog.) and Mt Welirang (Van Steenis 10949 in Herb. Bog.).

var. *bifida* nov. var.

Apex lemmae bifida, uterque dens aristatus, aristis c. 1 mm longis. Panicula magna, usque 35 cm longa, erecta et patentissima.

Distr. Java: Mt Slamat (Van Steenis 11631 in Herb. Lugd. Bat.).

8. **Deyeuxia archboldii** (Hitchc.) Jansen, nov. comb.

Calamagrostis archboldii Hitchc. Brittonia *2* : 115. 1936.

Distr. Only known from N. Guinea, Murray Pass (Brass 4570 & 4592).
Ecol. Open grasslands at 2800 m altitude.

9. **Deyeuxia pusilla** (Reeder) Jansen, nov. comb.

Calamagrostis pusilla Reeder, J. Arn. Arb. *31* : 322. 1950.

Distr. New Guinea, Morobe district and Lake Habbema.
Ecol. With other dwarf grasses on wet boggy ground, 3000 to 3500 m altitude, each plant forming a distinct tuft.

DICHANTHIUM Willemet.

Dichanthium erectum Ohwi, Bull. Tokyo Sc. Mus. 18: 11. 1947.

The following is an emendation of the short original description: Perennial on a short hard rhizome without stolons. Culms 30—60 cm high, simple, erect, wiry, very slender, many-noded, glabrous and smooth. Sheaths shorter than the internodes, tight, terete, glabrous, closed nearly to the tip. Ligule very short to nearly absent. Blades rather stiff, those of the innovations and the lower culm-blades erect, the upper more spreading, linear, flat, rounded at the base, 3—4 cm long, 2—4 mm wide, glaucous, glabrous to sparsely tubercle-based hairy near the base. Panicle reduced to one long-exserted raceme, 3—5 cm long, rather loosely spikeled, 5—10 articulated, the slender joints 3—2$^1/_2$ mm long, ciliate along the margins and at the tip. Lower 2—4 spikelets male or reduced, awnless. Sessile spikelets lanceolate to elliptic, 4$^1/_2$—5 mm long, the base white-bearded. First glume as long as the spikelet, lanceolate-elliptic, acute, very narrowly winged, the keels minutely ciliolate towards the tip, indistinctly 6—7-nerved. Second glume as long, obtusish or minutely mucronate. Sterile lemma 3 mm long, hyaline, unnerved. Fertile lemma nearly reduced to a twice geniculated awn, 15—20 mm long. Pedicels 1$^1/_2$ mm long, ciliate along the margins and at the tip. Pedicelled spikelets male or neuter, awnless, the first glume often with one or more pits.

Distr. Timor (Walsh 45, typus; Walsh 32; Monod de Froideville 1242). Sumba (Hoekstra 13; Iboet 209).
Ecol. On calcareous hills, 700—800 m altitude.

This species differs from one-racemed specimens of *D. caricosum* in the wiry, erect culms, the stiff, short blades, the loosely spikeled raceme with long, tender joints, the nearly glabrous, indistinctly nerved and very acute first glume of the sessile spikelets. The type-sheet contains both specimens with unpitted and with 1—3-pitted pedicelled spikelets. In the specimen Walsh 32 (in Herb. Br. Mus. London) most of the pedicelled spikelets are unpitted, whereas some of them show a series of pits. Monod 1242, though apparently representing the same species, differs from the type by higher, more or less straggling, very wiry culms (those of the innovations are strictly erect), very glaucous, stiff, short blades which are erect in the innovations and the lower part of the culms but spreading in the upper part. The spikelets are unpitted.

Dichanthium mucronulatum Jansen nov. sp.

Perenne, laxe caespitosum. Culmi rigide erecti, usque ad 80 cm alti, teretes, glabri et laeves, nodis glabris, ab nodis superioribus ramosi. Vaginae glabrae, breviores quam internodia, inferiores subcompressae et laxae, superiores angustae. Ligula membranacea, c. 1 mm longa, truncata. Laminae lineares, paullo angustatae basin versus, apice longe acuminatae, molles, planae, nervo medio forti

inferne albescenti, marginibus laevibus, subglaucae, glabrae vel pilis longis sparsiter indutae. Inflorescentia elongata, erecta; racemi solitarii et terminales in culmis et ramis. Racemi 5—6 cm longi, 5 mm lati, virides; articulis et pedicelli filiformibus, solidis, c. 1 mm longis, prope basin glabris, apicem versus per margines ciliatis, pilis superioribus longioribus. Spiculae lineari-oblongae, 5—6 mm longae, pares 2—3 inferiores steriles vel ♂ et inermes; callus brevis, dense pilosus. Gluma I dorso rotundata, plurinervosa, glabra, minute ciliata per margines anguste inflexas apicem versus, mucronulata, nervo medio paullo exserto. Gluma II primam aequans, acuta vel minuta bidentata, glabra. Lemma sterile obtusum, valde brevior quam glumam. Lemma superior ad stipem hyalinum reductum, in aristam geniculatam 3 cm longam transiens, columna aristae laxe torta. Antherae lineares, minutae. Caryopsis oblonga. Spiculae pedicellatae c. sessiles aequantes, ♂ vel steriles, glabrae et inermes.

Distr. Mal. Peninsula; Gira Bate (Ridley 8129), typus in Herb. Singapore. Ecol. On rocks at low altitude.

A nearly glabrous species differing from *D. annulatum* (Forsk.) Stapf in the strictly erect, tall culms, the solitary racemes terminating the culms and their branches, the narrower and longer spikelets with a glabrous distinctly mucronate lower glume, and the long awn with a slightly wavy stipe and a loosely geniculate and twisted column.

ECTROSIOPSIS (Ohwi) Jansen

Ectrosiopsis curvifolia Jansen nov. spec..

Gramen annuum, caespitosum. Culmi gracillimi et tenaces, erecti, 30—40 cm alti, pleraque folia ad basin conferta, hirsuti pilis minute basi-tuberculatis, albis, patentibus, c. 1 mm longis. Vaginae inferiores elaminata, rudimenta breviora quam internodia, laxa, hirsuta pilis mox caducis basi-tuberculatis. Ligula ad pilos brevissimos seriatim confertos reducta. Laminae anguste lineares, usque ad 20 cm longae et 2—$2^1/_2$ mm latae per partem dimidiam basalem, apicem versus attenuatae ad partem superiorem curvatam, involutam, acutissimam, hirsutae superne et inferne pilis basi-tuberculatis, densissimis prope basin. Panicula elongata, 10—15 cm longa, axis ramis et pedicellis hirsutis pilis patentibus; rami solitarii et distantes (internodia inferiora 5—3 cm longa), oblique erecti sive patentes, inferiores 2—3 cm longi, 5—8 spiculas breve pedicellatas, magis minusve erectas, superiores gradatim breviores et spiculas pauciores gerentes. Spiculae lineari-oblongae, 6—7 mm longae, manifeste lateraliter compressae, pallide virides, glabrae, laeves. Glumae membranaceae, naviculiformes, inequales, inferior 1 mm longa, superior c. 2 mm longa, utraque acuta, 1-nervia, longe persistens; rhachilla inter flosculas disarticulans. Flosculorum 3 inferiores bisexuales; lemma membranaceum, rectum dorso, a latere visu ovatum, c. 2 mm longum, latior, in apice acuminata attenuatum, 3-nervium, nervis lateralibus ab medio cum ab margine aeque remotis. Lemma flosculorum superiorum sterilium longior et angustior, in apicem acuminatissimum breviter aristatum et recurvatum attenuatum. Antherae 0.3—0,4 mm longae. Caryopsis ellipsoideus.

Distr. New Guinea, Mai Kussa, leg. MacGregor a. 1890, No. 9 in Herb. Melbourne (typus).

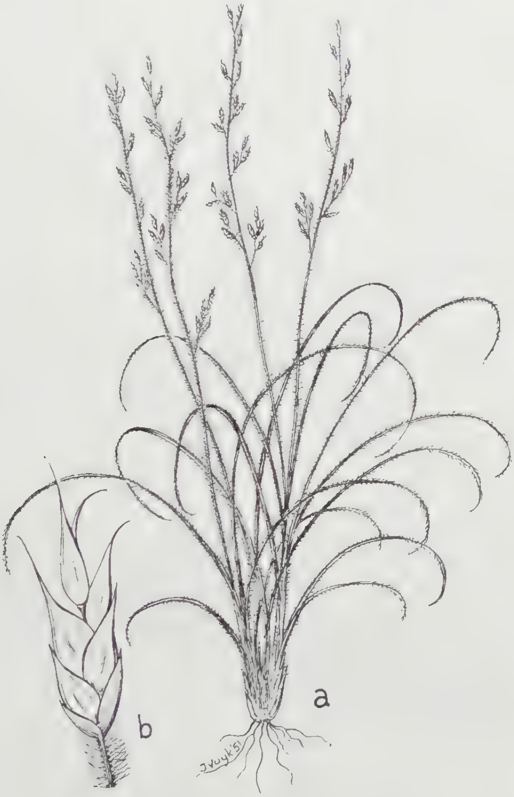


Fig. 2. Ectrosiopsis curvifolia
a. type from Mai Kussa. *b.* spikelet

SPOROBOLUS R. Br.

1. **Sporobolus javensis** Ohwi, Bull. Tokyo Mus. *18*: 12. (1947)

Backer (Handb. Fl. Jav. **2**: 205. 1928,) mentions the occurrence of *Sporobolus lindleyi* (Steud.) Bth. from East Java, where this species occurs on open brackish soil at the base of the hill Semongkrong. *Sp. lindleyi* Bth. is based on *Vilfa lindleyi* Steud., the latter being only a name change of *Sp. pallidus* Lindl. 1848, non Nees 1840. Nees originally gave the name to an Arabian grass, Lindley applied it for an Australian grass. Hooker f. discussed the nomenclatural position of *Sp. pallidus* in Fl. Br. Ind. *7*: 252. 1897,. He came to the conclusion that it was preferable to retain the name *Sp. pallidus* for

the Australian plant and to call the Arabian species *Sp. arabicus* Boiss. (Diagn. Pl. Or. *I*, 13, 1853, p. 14).

C. E. Hubbard examined Lindley's type specimen in Herb. Univ. Cambridge and stated *that it represents Eragrostis japonica* (Thunb.) Trin. Therefore, Bentham's name *Sp. lindleyi* (Steud.) Bth. can no more be used for this Australian species.

The next synonym of it is *Sp. subtilis* F. v. M., but this is a homonym of a different species described by Kunth. S. T. Blake concluded that the only available name for it is *Sp. caroli* Mez (in Fedde, Repert. **17**: 299. 1921).

The East Javan specimens do not at all agree with the Australian species (figured e. g. by Turner, Austral. Grass. 1895, p. 53) and I agree with Ohwi that it is specifically distinct, a view shared by Mr. Blake whom I sent specimens.

Likewise *Sp. javensis* is not nearly related to *Sp. australasicus* Domin (in Fedde, Repert. *9*: 53. 1911,) and to *Sp. coromandelianus* (Retz) Kunth (Rév. Gram. *1*: 68 1829,). *Sp. australasicus* is a more slender species with shorter relatively broader spikelets on longer widely spreading pedicels; the lower glume is relatively longer; *the grain is globular.* The margins of the blades are more strongly thickened and bear more numerous, much longer and stouter spine-like hairs.

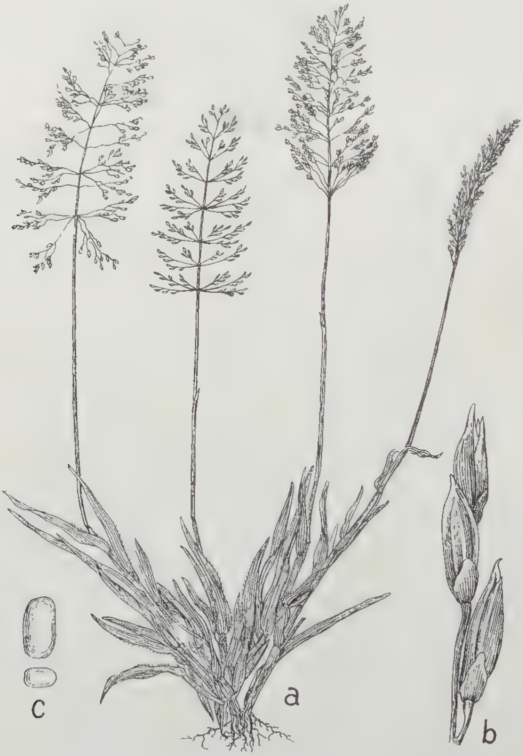


Fig. 3. Sporobolus javensis Ohwi
a. type from Java. *b.* spikelets. *c.* grain

Sporobolus coromandelianus has more or less the same habit but the pedicels are shorter, the first glume minute and the axis of the panicle is glandular above the first whorl.

Here follows a slightly emended description of *Sporobolus javensis* Ohwi.

Annual, caespitose. Culms geniculate-ascending to erect, simple, glabrous and smooth, 2—4-noded, 20—35 cm high. Lower sheaths short, subcompressed, glabrous, the margins ciliate; uppermost sheaths about 1 dm long and nearly bladeless. Ligule $^2/_3$ mm long, densely ciliate. Blades lanceolate-linear, flat and soft, 3—9 cm long, 4—8 mm wide, crowded at the base of the culms, the margins slightly thickened and ciliate with short, tubercle-based hairs, especially in the lower part. Panicle exserted, erect, oblong-ovate, 6—8 cm long, 3—4 cm wide, the filiform branches in distinct whorls, obliquely spreading, the lower 2,25—4 cm long, naked below for $^1/_3$—$^2/_3$ of their length, scabrid in the upper part, the spikelets tending to occupy only the outside of the panicle and shortly pedicelled, about 15 mm long, greyish to blackish. First glume short, $^1/_4$—$^1/_3$ the length of the spikelet, ovate, obtuse. Second glume as long as the spikelet, usually adpressed, when young scabrid to pilose in the upper part. Lemma slightly shorter than the second glume, 1-nerved. Palea shorter, obtuse, easily splitting up in 2 parts. *Grain obovate-truncate, subangular*, 0.8—0.9 mm long.

Distr. Only known from East Java.

Ecol. On open, sunny, brackish soil at the base of the hill Semonkrong (Van Slooten 2394, typus in Herb. Bogor.).

2. **Sporobolus lenticularis** S. T. Blake, Univ. of Queensl. Papers I, 18: 1941, p. 4.

Backer (Handb. Fl. Jav. *2*: 205. 1928) mentions *Sporobolus pulchellus* R. Br. to occur in Sumatra. I compared the Sumatran specimens with Brown's type in Herb. Kew. They certainly are different and represent another species.

Ohwi (Bull. Tokyo Sc. Mus. *18*: 12. 1947) described them as a new species: *Sporobolus sumatranus* Ohwi. Culms slender, up to 45 cm long; most of the leaves crowded at the base. Blades lanceolate-linear (when flattened out), more or less canaliculate and involute towards the acute tip, their margins pectinate-ciliate with bulbous-based hairs, especially towards the base. Panicle exserted, up to 12 cm long and 3—4 cm wide; branches arranged in distant whorls, spreading, naked at their base, simple or with short branchlets; spikelets short-pedicelled, tending to occupy the outside of the panicle. Spikelets glossy, red-brown, 1.5—1.7 mm long. First glume rather long, reaching $^1/_2$—$^2/_3$ the length of the spikelet, hyaline, acute, unnerved. Second glume as long as the spikelet, acute, 1-nerved. Lemma nearly as long, more obtusish, membranous, 1-nerved. Grain elliptic to lenticular, *laterally compressed with thin edges*.

This species agrees with the description of *Sporobolus lenticularis* S. T. Blake, l. c.. By courtesy of Mr. Blake I received a duplicate of the type number (Blake 13384, from Queensland) an examination of which sustained my opinion.

Distr. Australia, Malaysia: North Sumatra, Atjeh (Ostwald 77, Jeswiet 558 & 668), East Sumatra (Sohns 7, Bartlett 8343), Toba Plain (Lörzing 9869, Weiland a. 1920).

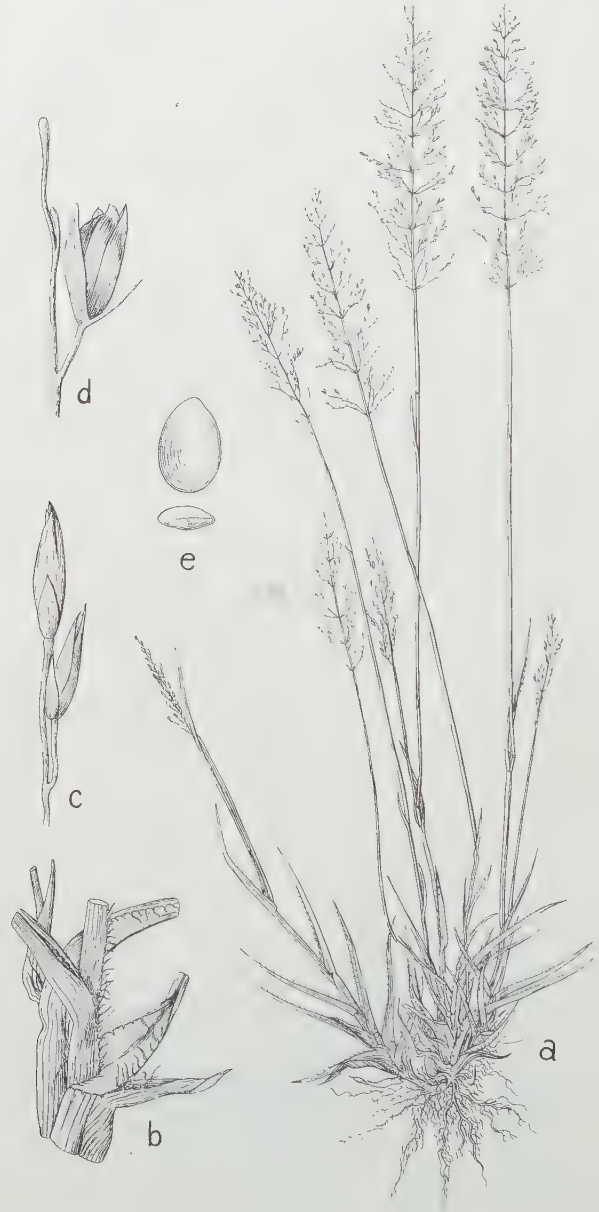


Fig. 4. Sporobolus lenticularis S. T. Blake *a.* specimen from Sumatra. *b.* lower sheaths. *c.* young spikelets. *d.* mature spikelet. *e.* grain

3. **Sporobolus virginicus** (L.) Kunth.

This species, a cosmopolitan, coastal, sand-dune plant with creeping rhizomes is very variably in habit, leaf-shape, and panicle.

Ohwi (Bull. Tokyo Sc. Mus. *18*: 1. 13. 947) described *Sporobolus sundaicus*, differing slightly from typical *S. virginicus*.

The type specimens in Herb. Bogor. do not possess stolons. However, the specimens of the same number in Herb. Leiden have long and freely branching stolons like in typical *S. virginicus*. They are strongly branched from the lower nodes; the shoots and branches erect, virgate, 20—40 cm high with numerous very narrow complicate blades, 7—12 cm long and 2 mm wide when expanded. The panicle is 7—12 cm long, contracted with erectly adpressed short branches. I see no difference in the spikelets: they are similar to those of typical *S. virginicus* save they are slightly shorter. Given the extensive distribution of *S. virginicus* it is evident that such slight deviations may be expected. They have at most varietal significance.

THEMEDA Forsk.

1. **Themeda arguens** (L.) Hack. D. C. Monogr. Phan. 6: 657. 1889, is based on *Stipa arguens* L., Sp. Pl. ed. 2 : 117. 1762, the specific epithet being derived from but not based on *Gramen arguens* Rumph., Herb. Amboin. *6* : 15. 1750, tab. 6 fig. 1. The Linnean description in one respect ("bracteis basi barbatis—Bracteae longiore basi extens valde pilosae") applies better to Hackel's conception of *Th. arguens* than to *Th. quadrivalvis* (L.) *O*. Kuntze, Rev. Gen. Pl. *2* : 794. 1891, based on *Andropogon quadrivalvis* L. In other respects it would apply well to both species. Merrill (Interpr. Herb. Amboin. 89. 1917) rejected the combination of Hackel and accepted the name *Th. frondosa* (R. Br.) Merr., based on *Anthistiria frondosa* R. Br. Prodr. 200. 1810. Probably he did not compare the type of *Stipa arguens* L. himself, at least he does not actually say so, but based his remarks on the interpretation of Munro. At my request Dr. C. E. Hubbard kindly examined the type in the Linnean herbarium. He states that it is definitely identical with *Th. arguens* as described by Hackel and not with *Th. quadrivalvis* (L.) O. Kuntze.

var. **balinensis,** var. nov..

Culmis brevibus gracilibusque folia angusta plicata gerentibus distincta. Vaginae glabrae nodis pubescentibus et ore longe ciliato exceptis. Panicula brevis fasciculis 1—2 pauco-spiculatis composita. Spathae et glumae glabrae vel sparsissime pilosae.

Distr. Bali (Van Steenis 7763a, typus), Timor (Monod de Froideville 1356), Sumba (Monod de Froideville 2009).

Ecol. On hot grassy slopes at 50—150 m altitude.

2. **Themeda quadrivalvis** (L.) O. Kuntze.

Hackel (DC. Monogr. Phan. *6* : 664. 1889) mentioned this species as *Th. ciliata* (L. f.) Hack., based on *Anthistiria ciliata* L. f. Suppl.

113. 1781. This is an illegitimate name as the younger LINNAEUS cited in his synonymy: *Andropogon quadrivalvis* L., Syst. ed. 13 p. 158.

Distr. Native of SE. Asia and the Seychelles, in Malaysia only known from Timor and Sumba. In Timor it grows in savannahs with no or few cattle and is subjected to annual burning.

The group of species taken together as *Th. gigantea* by Hackel, DC. Monogr. Phan. *6* : 670. 1889, has been split up again by STAPF, A. CAMUS and others. The Malaysian species may be divided in 2 series as follows:

A. Involucral spikelets densely hirsute with fulvous tubercle-based hairs.
  1. Each raceme with 1 fertile spikelet or very rarely 2.
    2. Fertile spikelet awnless or shortly and imperfectly awned. Involucral spikelets 5—7 mm long. 3. **Th. gigantea**
    2. Fertile spikelets with a long, hairy, perfect awn. Involucral spikelets 10—18 mm long. 4. **Th. arundinacea**
  1. Each raceme with 2—3 fertile spikelets with the awn reduced to a short, subule or wanting. 5. **Th. intermedia**

B. Involucral spikelets glabrous or scabrous.
  3. Each raceme with 2—4 fertile spikelets.
    4. Fertile spikelets 7—8 mm long, awnless or very shortly and imperfectly awned. 6. **Th. villosa**
    4. Fertile spikelets 9—11 mm long with a long, hairy, perfect awn. 7. **Th. caudata**
  3. Each raceme with 1 fertile spikelet.
    5. Involucral spikelets 12—15 mm long. Fertile spikelets brown-villous with a scabrous perfect awn. Sheaths glabrous and smooth. Panicle elongate, dense with long racemes. 8. **Th. idjenensis**
    5. Involucral spikelets shorter. Fertile spikelets scabrous, not villous, with a hairy perfect awn. Lower sheaths hairy. Panicle open with short racemes. 9. **Th. novoguineensis**

3. **Themeda gigantea** (Cav.) Hack., sens. str. in DC. Monogr. Phan. 6: 670. 1889.

Anthistiria gigantea Cav. Icon. *5* : 36. t. 458, 1799. *Androscepia gigantea* (Cav.) Brongn. Duperr. Voy. Bot. 78. 1829; Buse, in Miq. Pl. Jungh. 363. 1854, partly; Miq. Fl. Ind. Bat. *3* : 506. 1857, partly. — *Perobachne secunda* Presl, Rel. Haenk. *1* : 348. t. 48, 1830; Miq. Fl. Ind. Bat. *3* : 507. 1857. — *Th. gigantea* subsp. *genuina* var. *genuina* Hack. in DC. Monogr. Phan. *6* : 672. 1889; Merr. En. Philip. Pl. *1* : 50. 1923; Reeder, J. Arn. Arb. *29* : 373. 1948.

This species is characterized by its short densely hirsute racemes on a short peduncle with small involucral spikelets and one fertile spikelet (very rarely 2), with the upper lemma awnless or with a very short imperfect awn.

Distr. Restricted to the Philippines, where it is locally abundant in open grasslands and savannahs, at low and medium altitudes. Reeder l.c. mentions a specimen from the Solomon Islands (Brass 3518).

var. **vulpina** (Anderss.) Hack. l.c. 673.

Anthistiria vulpina Anderss. Nov. Act. *III*, 2 : 423. 1856.

The glumes of the involucral spikelets are densely bearded with golden or fulvous hairs based on whitish tubercles. The spikelets are slightly larger.

Distr. Only known from Luzon (Cuming 1272, type).
Note. This variety is of minor value.

4. **Themeda arundinacea** (Roxb.) A. Camus, in Lecomte, Fl. Gén. Indochine *7* : 363. 1922. — *Anthistiria arundinacea* Roxb. Fl. Ind. ed. Carey *1* : 251. 1820. — *Themeda gigantea* subsp. *arundinacea* (Roxb.) Hack., in DC. Monogr. Phan. *6* : 674. 1889; Back. Handb. Fl. Java *2* : 108. 1928.

This species differs from the preceeding in the large involucral spikelets up to 18 mm long, the upper lemma of the solitary fertile spikelet which has a perfect, geniculate, hairy awn, the pedicelled spikelets which are 8—12 mm long. The type of Anthistiria arundinacea in Herb. Br. Mus. London agrees perfectly with the Philippine specimens (e. g. Loher 1843).

Distr. India, Indochina, Malaysia: Philippines, W. Java, and Borneo (Motley 205).

var. *subsericans* (Nees ap. Steud.) A. Camus, in Lecomte, Fl. Gén. Indo-Chine *7* : 363. 1922.

Anthistiria subsericans Nees ap. Steud., Syn. *1* : 401. 1855. — *Themeda gigantea* var. *subsericans* Hack., l.c. 674. 1889. — *Themeda subsericans* (Nees) Ridley, Fl. Mal. Pen. *5* : 262. 1925.

Panicle-axis slightly pubescent, especially below the nodes. Peduncle of the racemes at the top often with long spreading hairs. Spikelets slightly shorter. Column of awn about 3 cm long.

Distr. India, Annam, Malaysia: Mal. Peninsula, Sumatra, and Borneo.

5. **Themeda intermedia** (Hack.) Dur. & Jacks. Ind. Kew. Suppl. 1: 424. 1906.

Themeda gigantea subsp. *intermedia* Hack., in DC. Monogr. Phan. *6* : 675. 1889. — *Themeda gigantea* var. *amboinensis* Hack. l.c. 673.

This species agrees with *Th. gigantea* in the hairy glumes and with *Th. villosa* in having racemes with 2—3 fertile spikelets. The hairiness of the glumes is usually less dense than in *Th. gigantea* and *Th. arundinacea*, the tubercle-based hairs vanishing upwards. The fertile spikelets, the blunt callus included, are about 10 mm long, the imperfect awns are usually reduced to the subule, very rarely they are perfect.

Distr. Malaysia: not yet from Sumatra and Java.

var. **intorta** var. nov.

Racemis spiculas hermaphrodita binas fere semper gerentibus distincta. Spiculae hermaphroditae perfectae aristatae, aristis flexuosis, ad se invicem intortis.

Distr. SE. Borneo (Van Loenen 16, typus, Neth. Ind. For. Serv. 59).

6. **Themeda villosa** (Poir.) Dur. & Jacks., Ind. Kew. Suppl. 1 : 424. 1906.

Anthistiria villosa Poir. Encycl. Suppl. 1 : 396. 1810. — *Heterolytron scabrum* Jungh. Tijdschr. Nat. Gesch. *7* : 294. 1839. — *Anthistiria mutica* Hassk. Tijdschr. Nat. Gesch. *7* : 117. 1843. — *Androscepia gigantea* Brongn. var. *sundaica* Buse, in Miq. Pl. Jungh. 364. 1854. — *Androscepia gigantea* Brongn. var. *mutica* Anderss. Nov. Act. Upsal. *III, 2* : 248. 1856. — *Themeda gigantea* subsp. *villosa* Hack., in DC. Monogr. Phan. *6* : 675. 1889; Back. Handb. Fl. Java *2* : 108. 1928.

This is among the tall species the most common one in Malaysia. It is characterized by the short racemes with 2—3 (rarely 4) densely brown-villous fertile spikelets, 7—8 mm long. The involucral spikelets with glabrous or rarely scabrous glumes are up to 10 mm long. The fertile lemma is awnless or very shortly and imperfectly awned.

Distr. Throughout Malaysia.

7. **Themeda caudata** (Nees) Dur. & Jacks. Ind. Kew. Suppl. 1 : 424. 1906; A. Camus, in Lecomte, Fl. Gén. Indo-Chine 7 : 364. 1922; Honda, Bot. Mag. Tokyo *40* : 108. 1926; Bor, Fl. Assam *5* : 410. 1940.

Anthistiria caudata Nees in Hook. & Arn., Bot. Beech Voy. 245. 1838. — *Themeda gigantea* subsp. *caudata* Hack., in DC. Monogr. Phan. *6* : 676. 1889; Merr., Bibl. Enum. Born. Pl. 42. 1921.

Closely allied to *Th. villosa* but differing in the longer fertile spikelets (9—11 mm); lower glume very coriaceous, nearly covering the second; the upper lemma with a perfect, hairy, geniculate awn 4—8 cm long.

Distr. Malaysia: not yet recorded from the Philippines, Moluccas, and New Guinea.

8. **Themeda idjenensis** nov. spec.

Themeda gigantea subsp. *avenacea* (non Hack.) Back. Handb. Fl. Java *2* : 108. 1928.

Ab *Th. villosa* differt robustiore usque ad 5 m altum, perglabrum et laeve. Panicula longissima et angustissima, ramis saepe dense fasciculatis. Spatheae angustissimae, implerisque breviores quam racemos. Racemes usque ad 2 cm longi, spiculam fertilem unam anguste lanceolatam et breviter pedicellatam agentes. Pedicellus glaber sive brevissime pilosus apice. Spiculae involucrales glabrae, 12—15 mm longae, longe acutissimae sive breve aristatae. Spicula fertile breviter brunneo-villosum, arista scabra, haud pilosa, geniculata, usque ad 6 cm longa, columna subulam superante.

Distr. East Java, gregarious on the northern slopes of the Idjen plateau and Mt Tenger (Koorders 42922, typus, Backer 25158, 36158, 36946; Beumée 1594; Bijhouwer 16).

This very robust species is quite glabrous and smooth. The elongate densely contracted, composite, spatheate panicle is up to 1 m long. The spathes of the racemes are very narrow and shorter than the racemes. The involucral spikelets with smooth, glabrous glumes are very long (12—15 mm) exceeding the solitary fertile spikelet. The awn of the upper lemma is only scabrous (not hairy), geniculate, about 6 cm long, the column much exceeding the subule.

9. **Themeda novoguineensis** (Reeder) nov. stat.

Themeda gigantea (Cav.) Hack. var. *novoguineensis* Reeder, J. Arn. Arb. *29* : 374. 1948. — *Themeda gigantea* (non Hack.) Hitchc. Brittonia *2* : 912. 1936.

This species belongs by its glabrous glumes of the involucral spikelets to the group of *Th. villosa*. It is characterized by whitish, long-pubescent lower sheaths and pubescent nodes and panicle. The spathes are $2^1/_2$ cm long and contain one fertile spikelet. The involucral spikelets are placed in 2 pairs, slightly distant from each other. The glumes of the fertile spikelet are only aculeolate-scabrous, but not villous. The hairy, perfect awn is 4—5 cm long.

Distr. New Guinea (Brass 3710, typus, Brass 3589, Carr 11235, Armit 44, Chalmers a. 1883 in Herb. Melbourne) and Celebes (Eyma 14681).

Ecol. Often the main contingent of grassy vegetation on mountain slopes at medium altitudes.

IN MEMORIAM ABRAHAM WILLEM KLOOS

DOOR

P. JANSEN (Amsterdam)

3 Juni 1952 stierf hij, 72 jaar oud.

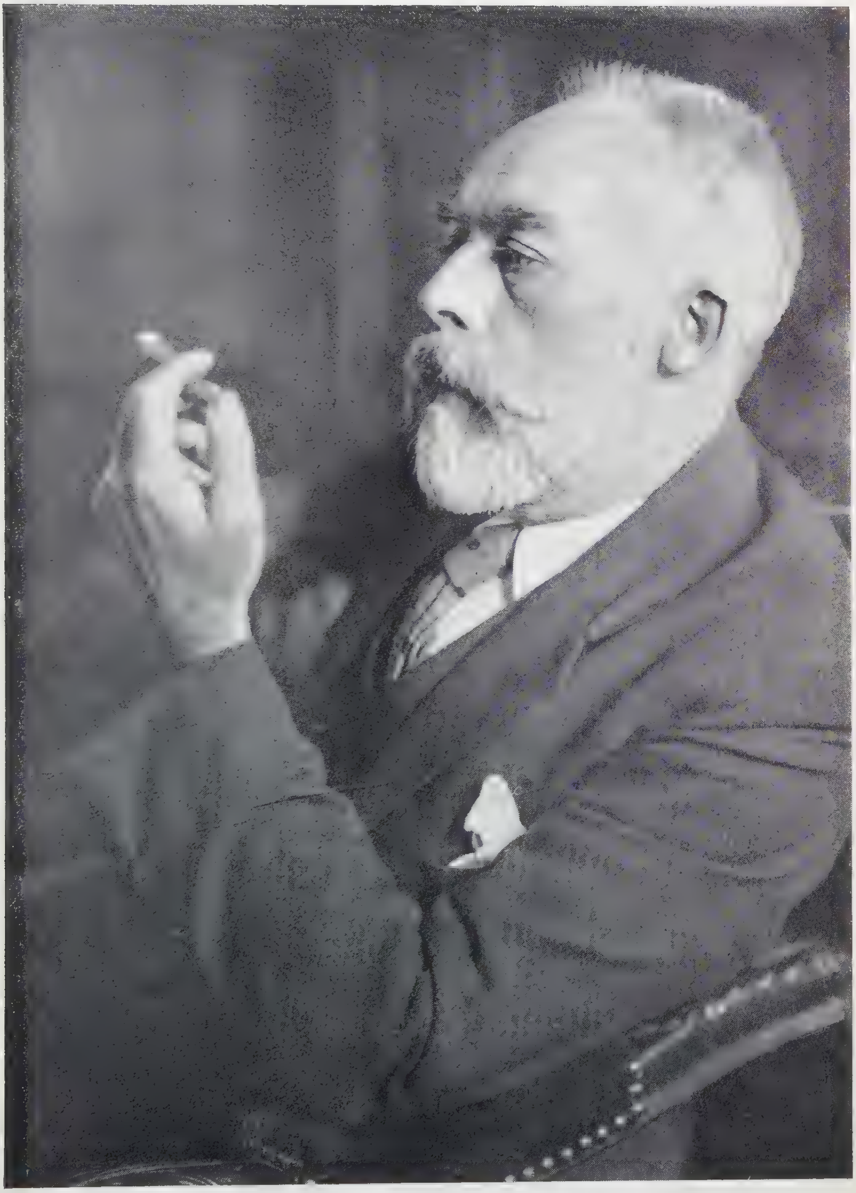
De Jaarvergadering der Vereniging in Januari heeft hij nog bijgewoond, zijn laatste financieel overzicht gegeven en zijn laatste begroting verdedigd. Toen hij thuis kwam voelde hij zich ziek. Snel verergerde zijn toestand, zodat hij in het ziekenhuis moest worden opgenomen. Een zware operatie heeft hem niet kunnen redden. Na een korte opleving kwam de terugslag en spoedig daarna het einde.

Terwijl ik dit schrijf hangt tegenover mij zijn portret met zijn scherpe en toch zo zachtmoedige blik: ogen die welbehaaglijk konden glanzen en geestig twinkelen. Het is een moeilijk realiseerbaar feit, dat hij mij nooit meer zal aankijken. Er is iets weggebrand uit mijn hart. En dat moet het geval zijn bij allen die hem kenden, bij al zijn leerlingen, bij allen voor wie hij een floristisch mentor is geweest.

Hij was Delfts Ingenieur en is leraar in de wiskunde en mechanica geweest aan de Dordse M.T.S., waaraan hij vanaf de oprichting tot aan zijn pensioenering in 1945 verbonden is gebleven. Hij behoorde tot de pioniers op dat gebied van het onderwijs. Zijn onderrichtscapaciteit kan moeilijk overschat worden. Een vak als mechanica, dat zo droog kan zijn, werd onder zijn handen levend en interessant.

40 Jaar zijn wij vrienden geweest en de eerste maal, dat ik hem sprak, staat mij nog even helder voor de geest als de laatste. Die eerste maal viel op een voorjaarsavond in 1912, toen hij mij kwam opzoeken: een slanke man met een zwarte ringbaard, de haren van zijn kuif rechtopstaand boven een hoog voorhoofd. Hij kwam advies inwinnen omtrent enkele door hem in de omgeving van Goes, zijn eerste standplaats, verzamelde planten en tevens raad vragen over de inrichting van een wetenschappelijk herbarium. Nog geen uur hadden wij met elkander gepraat, of wij wisten dat wij vrienden zouden worden, verbonden door de banden, die zich tussen liefhebbers der vrije natuur als het ware van zelf vormen.

De laatste maal viel in Mei 1952, een heerlijke voorjaarsmorgen, toen hij mij over de Nieuwe Weg zag aankomen en mij in tuincostuum op zijn klompen tegemoetkwam, de beide handen naar mij uitstekende. Hij scheen herstellende van de zware operatie, al was zijn gezicht nog doorploegd van de ellende, die hij had doorstaan. Samen hebben wij die morgen onder de warme voorjaarszon in zijn tuin doorgebracht, waar honderden planten uitliepen of reeds bloeiden, allerlei merkwaardigheden bekijkend en besprekend, niet wetend dat het de laatste maal zou zijn. Zo goed voelde hij zich toen, dat



A. W. KLOOS †

hij al plannen maakte om, desnoods met een auto, de zomerexcursie mee te maken.

Tussen beide ontmoetingen liggen 40 jaar van vriendschap en samenwerking.

In 1912 werd Kloos lid der Ned. Bot. Vereniging. Dat was juist in de tijd na de reorganisatie, zo treffend door Wachter in het Gedenkboek beschreven, de tijd waarin de floristiek uit het verenigingsleven dreigde te verdwijnen. Hij nam dadelijk deel aan het werk der toen opgerichte Floristische Club en hield op de eerste vergadering in Leiden reeds een voordracht over afwijkende vormen van Salix en Viola. Nadat in 1913 de Commissie voor het floristisch onderzoek het recht kreeg zelfstandig te vergaderen en ruimte kreeg om floristische mededelingen te publiceren werd deze Club overbodig. In 1917 werd Kloos lid der Commissie. Door zijn vele excursies, waarvan een steeds groeiend herbarium het gevolg was, nam zijn kennis der flora zo toe, dat hij onbetwist de grootmeester der Nederlandse floristen werd. Toen dan ook Vuyck in de laatste jaren van zijn leven niet meer op de excursies aanwezig was, werd Kloos aangewezen die excursies te leiden (de eerste in 1924 naar Eysden). Na Vuycks overlijden in 1931 was hij diens aangewezen opvolger en sinds die tijd heeft hij bijna alle zomerexcursies voorbereid, geleid en van de meeste een verslag gegeven in het Ned. Kr. Archief. Op die excursies was hij leider en makker tevens, onvatbaar voor weers- en andere invloeden, onvermoeid en onverstoorbaar van humeur. Ik

Op excursie in 1952

heb hem slechts eenmaal boos gezien, op de excursie naar Coevorden, toen hij meende, dat enige jongeren trachtten hem de leiding uit handen te nemen. Dit bleek gelukkig een misverstand en de vrede was dadelijk getekend. Ik zie zijn karakteristieke figuur nog, meest in een wit of lichtgrijs costuum, dat tegen het einde der excursie alle kleuren van de regenboog vertoonde; zijn witte plantentrommel met speciaal voor hem gesmede plantenschop. Want hij verzamelde niet alleen voor zijn herbarium, maar groef vele merkwaardigheden uit, om ze in zijn tuin te kweken. Begaafd met een scherpe blik wist hij alle soorten op te sporen, die in het onderzochte gebied moesten of konden voorkomen. Zo was het lange tijd zijn hobby, om overal waar hij kwam naar Centunculus minimus te zoeken, die voor zeldzaam doorging, en hij slaagde er bijna altijd in deze voor vele floristen onvindbare plant te ontdekken. Naast deze officiële zomerexcursies leidde hij meestal ook een Pinksterexcursie, liefst naar het Zuiden van ons land, waarbij met HENRARD, WACHTER en mij, na het uitvallen van HENRARD met ons drieën en later met een klein gezelschap intensief werd gewerkt. Vroeg opstaan was daarbij niet zijn sterke kant. Zo herinner ik mij een excursie in Houthem, waarbij hij 's morgens in bed bleef, totdat de trein in Meersen affloot en dan speelde hij het nog klaar om juist op het nippertje met zijn ontbijt in de hand de laatste coupé binnen te stappen. Maar als wij van een vermoeiende dagtocht terug waren, dan moest en zou de rest van de avond besteed worden aan uitzoeken, inleggen en critisch bespreken van het verzamelde materiaal, dikwijls tot laat in de nacht. Gewoonlijk kwamen wij dan na enige weken nog eens bij hem thuis samen, om onze resultaten te vergelijken. Zo werd, met medewerking van zijn vrouw, zijn huis aan de Nieuwe Weg te Dordrecht een floristisch asyl. Hoevelen heeft hij daar met onuitputtelijk geduld spoorwijs gemaakt en geholpen! Hoevelen heeft hij in zijn tuin de verschillen getoond tussen verwante soorten en ze aangemoedigd hun onderzoek voort te zetten? Altijd stond hij klaar zijn uitgebreide kennis ten dienste te stellen van een ernstige zoeker. Ook de kleinste onopgeloste kwestie bleef zijn aandacht vast houden, zodat het kon gebeuren van hem een brief te ontvangen, waarin de oplossing stond van een hem jaren geleden voorgelegd raadsel. Was het wonder dat hij het geestelijk middelpunt werd van floristisch Nederland?

Daarnaast wierp hij zich op het onderzoek van vele moeilijke en vormenrijke geslachten. Zijn vele artikelen in Ned. Kr. Archief, in De Levende Natuur, zijn tabellen in de geïllustreerde Flora van HEIMANS en THYSSE, zijn werk voor de Flora Neerlandica getuigen alle van zijn scherpe blik, zijn literatuurkennis en zijn vermogen om moeilijke kwesties duidelijk uit te leggen. Dank zij zijn talrijke bezoeken aan allerlei adventiefterreinen verwierf hij zich een enorme soortenkennis. De talrijke raadsels, welke deze planten hem stelden, loste hij eerst op met behulp van zijn leermeester en vriend ALB. THELLUNG, later zelfstandig met raadpleging van de schatten in 's Rijks Herbarium.

Zo werd hij tot autoriteit en vraagbaak voor allen, die in adventieven belang stelden, waaronder vele bekende botanici uit alle delen der wereld. De resultaten publiceerde hij als „Aanwinsten" in het Kr. Archief. Zij bevatten beschrijvingen en discussies van honderden soorten, waaronder vele nieuwe vormen en zij zullen steeds een onuitputtelijke bron blijven voor de geschiedenis der Nederlandse floristiek vanaf 1914. De eerste 27 deeltjes, lopende van 1914—1944, met het register saamgebonden, vormen een boek van meer dan 600 paginas. In Archief 57 en 58 werd deze serie voortgezet en in de eerste aflevering van de Acta Botanica Neerlandica vindt men nog een uitvoerig overzicht van de aanwinsten tot en met 1950. Tot enige dagen voor zijn dood was hij, te bed liggend, nog bezig met de aanwinsten van 1951.

Ook als voorzitter der Paas- en Kerstvergaderingen was Kloos een opvallende figuur. Wie ziet hem niet de zaal binnenkomen met zijn steeds in een zwart zeil verpakte portefeuille, een hoorn des overvloeds, waaruit hij naar alle zijden voor de aanwezigen gedetermineerde planten uitdeelde? Wie ziet hem niet de hamer opnemen en langzaam met iets gebogen hoofd een informele, meest geestige inleiding houden? Wie ondervond niet zijn bindende invloed, nooit scherp tegenover personen maar wel scherp tegenover planten? Het zijn mensen als Kloos, die van de floristische bijeenkomsten een vriendenkring hebben gemaakt.

In nog vele andere functies maakte hij zich verdienstelijk jegens de Vereniging. Als lid der Herbarium-commissie controleerde hij zelf de determinaties van alle ingezonden planten, zodat de volledige commissie slechts de resultaten van zijn werk had te beoordelen. Als lid der Zuiderzee Commissie hielp hij o.a. mee aan het onderzoek van Wieringen en de Balgzandpolder. Onze laatste Zuiderzee-excursie gold het onderzoek der Phragmites-vegetatie in de N.O. Polder in 1946. Vanaf 1926 was hij lid van de Commissie voor Bibliotheek en Herbarium, terwijl hij als lid der redactie voor de Flora Neerlandica de uitgave sterk stimuleerde en veel werk er voor verzette. Verder was hij van 1928—32, van 1938—42 en van 1949 tot aan zijn dood penningmeester der Vereniging. Naast J. G. Sloff was hij de voornaamste medewerker van de I.V.O.N en hij werd door de Bot. Society of the Brit. Isles in 1950 uitgenodigd om op haar "Conference on the study of the distribution of British plants" een voordracht te houden over de Nederlandse wijze van kartering.

Geen wonder dat de Vereniging hem ter gelegenheid van de viering van het honderdjarig bestaan het erelidmaatschap aanbood. Hij had dat zeker verdiend en stelde het zeer op prijs. Ook de officiële botanische wetenschap waardeerde zijn werk, door hem op 10 Januari 1946 het doctoraat honoris causa te verlenen. Dit viel juist in een periode van geestelijke depressie, die hem tegen het eind van de oorlog was overvallen. Twee van zijn zoons hadden het leven verloren door toedoen van de Duitsers. De talrijke bewijzen van waardering en vriendschap, die hij bij deze gelegenheid uit binnen- en buitenland ontving, deden hem zijn oude veerkracht weer terug vinden.

Nadat hij van de M.T.S. afscheid had genomen, werd hij honorair medewerker aan 's Rijks Herbarium en begon hij aan een monografische behandeling van het geslacht Amaranthus. Hij bezocht daartoe enkele buitenlandse Herbaria en determineerde het materiaal uit talrijke andere. Ofschoon hij enige voorlopige resultaten publiceerde is het werk niet geheel gereed gekomen. Moge er een systematicus te vinden zijn, die er de laatste hand aan wil leggen.

De zesde Juni 1952 is hij te Westerveld verast, waarbij vele vrienden, oud-leerlingen en bekenden hem de laatste eer bewezen. De talrijke uitingen van rouw over zijn heengaan, van waardering voor wat hij tot stand bracht, van dankbaarheid voor zijn hulp en vriendschap zijn verklonken.

Maar hij zal, zolang er nog floristen leven die hem hebben gekend, niet verzinken in de afgrond van de tijd, want de herinnering aan hem zal hen bij hun werk en op hun excursies blijven vergezellen.

Juli 1952.

NOTES ON THE POTAMOGETONES OF THE ZUIDLAREN LAKE AND ITS ADJACENT WATERS

BY

E. W. CLASON (Groningen)

(*Received June 30, 1952*)

More than half a century ago Vuyck (1895, p. 630) urged the need of a renewed investigation of the occurrence and distribution of Potamogetones in the northern provinces of the Netherlands. Judging from the localities recorded by Kloos (1936), it is obvious that this recommendation is still actual, especially so for the province of Groningen. Whilst Potamogetones occur there in almost every water, on the maps of Kloos (l.c.) only a small number of squares is marked. Therefore I collected in the summer of 1950 the Potamogetones of the Zuidlaren Lake and some adjacent waters, situated about 10 km S of the city of Groningen. Potamogetones of this greatest oligohaline lake of the Netherlands were mentioned earlier by Havinga (1919, p. 14; this paper contains ample general information on the Lake) and by Clason (1928, II, p. 42). However, some species found by Havinga I could not find again, also some species I found in 1928 were not collected in 1950 and with some other species happened just the reverse. Kloos (l.c.) does not record any species from the Lake; however, on his maps the square comprising the lake-area is crossed for *P. natans* L., *P. lucens* L. and *P. oblongus* Viv. (= *P. polygonifolius* Pourr.). In the following notes I stick to the nomenclature and the descriptions of Ascherson and Graebner (1913); numbers refer to table I.

1. **P. natans** L. var. **prolixus** Koch.

Easily recognizable, especially by 4—5 mm high fruits. The plants found in the Lake and its vicinity have very constantly the following features: ligules considerably shorter than the petioles; floating leaves small (30—40 mm wide and 40—70 mm long); petioles long, often twice and more the length of lamina, in fresh condition not furrowed on the upper-side; lamina passing decurrently into the petiole, the transition marked by two small puckers only.

By no means abundant in the Lake; only in sheltered corners and in pools of open water in the *Scirpeto-Phragmitetum*, where the bottom is muddy, it is regularly found. In adjacent canals and ditches this same variety is very abundant.

2. **P. polygonifolius** Pourr.

Fruits only 2 mm high. I could not find it in 1950. A herbarium-specimen which I collected in 1928 under that name, proved to belong to *P. natans* L. var. *prolixus* Koch. No other herbarium-material available; the occurrence of this species must be considered uncertain.

According to local Dutch floras, this species should be confined to oligotroph waters (e.g. Heimans c.s., 1950, p. 194, states: "in heath-pools"). On the map of Kloos (l.c., p. 569) the majority of the habitats in the Netherlands is situated on higher grounds, indicating poor waters. However, round about the city of Groningen the map shows a coherent area, including the Lake-area, where nowadays oligotroph waters are very rare. As Havinga (l.c., p. 14) mentions the species from the Lake, it may have disappeared in recent times, because the water of the Lake became more eutroph in consequence of intensive manuring and progressing industrialisation of the hinterland.

TABLE I
Western-european Potamogetones according to Ascherson & Graebner and the available data about their occurrence in the Zuidlaren Lake and adjacent waters.

Sections and species	Havinga 1919	Clason 1928	Kloos 1936	Clason 1950
I. HETEROPHYLLI				
1. natans L.	×	× h	O	O × h
2. polygonifolius Pourr.	×	× ?	O	
3. fluitans Roth				
4. coloratus Vahl				
5. alpinus Balbis				
6. perfoliatus L.		×		O × h
7. praelongus Wulfen		O h		
8. lucens L.		×	O	O × h
9. zizii Mertens & Koch				× h
10. gramineus L.	×			
(11.) nitens Weber				
II. BATRACHOSERIS				
12. crispus L.		O		O h
III. CHLOËPHYLLI				
13. compressus L.				O × h
14. acutifolius Link.				O h
15. obtusifolius Mertens & Koch				× h
16. mucronatus Schrad.		× ?		
17. pusillus L.				O × h
(18.) rutilus Wolfgang				
19. trichoides Chamisso & Schl.				
IV. COLEOPHYLLI (PECTINATI)				
20. pectinatus L.	×	×		× h
(21.) filiformis Pers.				
V. ENANTIOPHYLLI				
22. densus L.	×			

× = in the Lake; O = in adjacent waters; h = in the Herbarium of the State University, Groningen; ( ) = not (yet) found in the Netherlands.

6. **P. perfoliatus** L.

In spring shoots show at the base internodes of 8 cm, blades oval to oblong, up to 7 cm long; farther above internodes shorter and blades smaller. Lateral shoots show very variable habits, obviously connected with the growing circumstances, viz. in periods of foulness of the water by water-bloom (abundant development of algae) and towards the end of growing-season they develop thin stems with small leaves. Margins of older blades not serrate, only very young not yet fully unfolded leaves have a somewhat rough margin. Kloos (l.c., p. 527) has described the leaf-margin as finely-serrate, however, this does not hold good for the plants of the lake.

Most common species of the open water of the Lake, also the most striking species. In small to very big patches, mostly in shallow places with a sandy bottom, but also very common in deeper places (to about 1.75 m), sometimes with a peaty bottom.

7. **P. praelongus** Wulfen.

In 1923 growing in the peaty mill-canal, which discharges via the Noordlaren canal into the Lake. In 1950 I could find it no more. A herbarium-specimen has leaves 10—15 cm long and up till 2.5 cm wide.

8. **P. lucens** L.

Leaf-form distinctly connected with growing circumstances, cf. Kloos, l.c., p. 537. In deep water, with rising water-level and with streaming water leaf long with long tapering point. In shallow, stagnant water with falling waterlevel leaf shorter with small point only. So the blades are oblong to lanceolate, cf. var. *vulgaris* Cham.; shoots with smaller, oval blades correspond more with var. *nitens* Cham. However I found these blades on shoots of the same plants, due to changing circumstances during the season.

In some places in fairly thin patches in the open water of the lake and also more regularly in sheltered corners and pools of the *Scirpeto-Phragmitetum.*

9. **P. zizii** Mertens et Koch (fig. 1, A 1—5).

According to Kloos (l.c., p. 539) this species has not been found with certainty in the Netherlands up to now. An important charac-

Leaves numbered from apex of shoot	Lamina		Unlaminate petiole long mm
	long mm	wide mm	
1. first fully unfolded	77	25	15
(1. idem *P. lucens*)	(90)	(24)	(2)
2.	78	26	14
3.	78	24	9
4.	(damaged)		
5.	73	18	2
6.	73	16	2
(6. *P. lucens*)	(99)	(25)	(2)

teristic is, that the uppermost leaves have longer petioles than the lower ones. I took the following measurements of leaves from a non flowering shoot; two measurements of corresponding leaves of a shoot of *P. lucens* L. (cf. var. *nitens* Chamisso) of the same locality have been inserted for sake of comparison.

All parts of *P. zizii* are less robust than the same parts of *P. lucens* growing next to it. Further features of *P. zizii* of the Zuidlaren Lake are the following. Lateral nerves unite with mid-nerve near base of blade, the outermost nerves last of all; alternately this union happens gradually resp. with a final curve to the mid-nerve. No well developed maze formed by very small nerves along the mid-nerve, only one such a small nerve on both sides along the mid-nerve. Peduncles are not thickened towards the top at flowering time, whereas this thickening happens to a considerable degree after the fruits have set. Well developed fruits to 3 mm high and almost as wide, distinctly flattened with a slightly convex to almost straight ventral suture and short apex. *P. lucens* of the same locality has 4—5 mm high fruits and these are more rotund, caused by a distinctly convex ventral suture. Ligule of *P. zizii* usually more pointed than that of *P. lucens*. I did not find floating leaves, otherwise the plants correspond to the variety *validus* Fieber.

In the S-E-edge of the Lake in sheltered corners with a sparse vegetation of emerging plants (*Scirpus lacustris* L., *Nymphaea alba* L. and *Nuphar luteum* Sm.).

12. **P. crispus** L.

The absence of this species in the Lake-area is embarrassing, as in the adjacent waters it is found abundantly.

13. **P. compressus** L.

Well developed leaves usually 3 mm wide; a mid-nerve and a parallel smaller nerve along both margins; between these 3 nerves a greater number of very fine nerves which unite near the apex with the mid-nerve. Apex narrows down fairly abruptly and ends in a small tapering point, fig. 1 B.

Very abundant in pools of open water with a muddy bottom amidst the *Scirpeto-Phragmitetum*; great patches of interwoven plants.

14. **P. acutifolius** Link.

Plants differ from *P. compressus* by the following features:

a. fully developed leaf usually not more than 2 mm wide, ending in a fine point, cf. var. *minor* Fieber. Venation same as that of *P. compressus*; however, the very fine nerves end in the parenchyma and do not unite with mid-nerve near the top, fig. 1 C.

b. peduncles shorter and fruits more rotund, higher (to 3 mm, against 2 mm for *P. compressus*). On the ventral side the fruit has usually some small knobs.

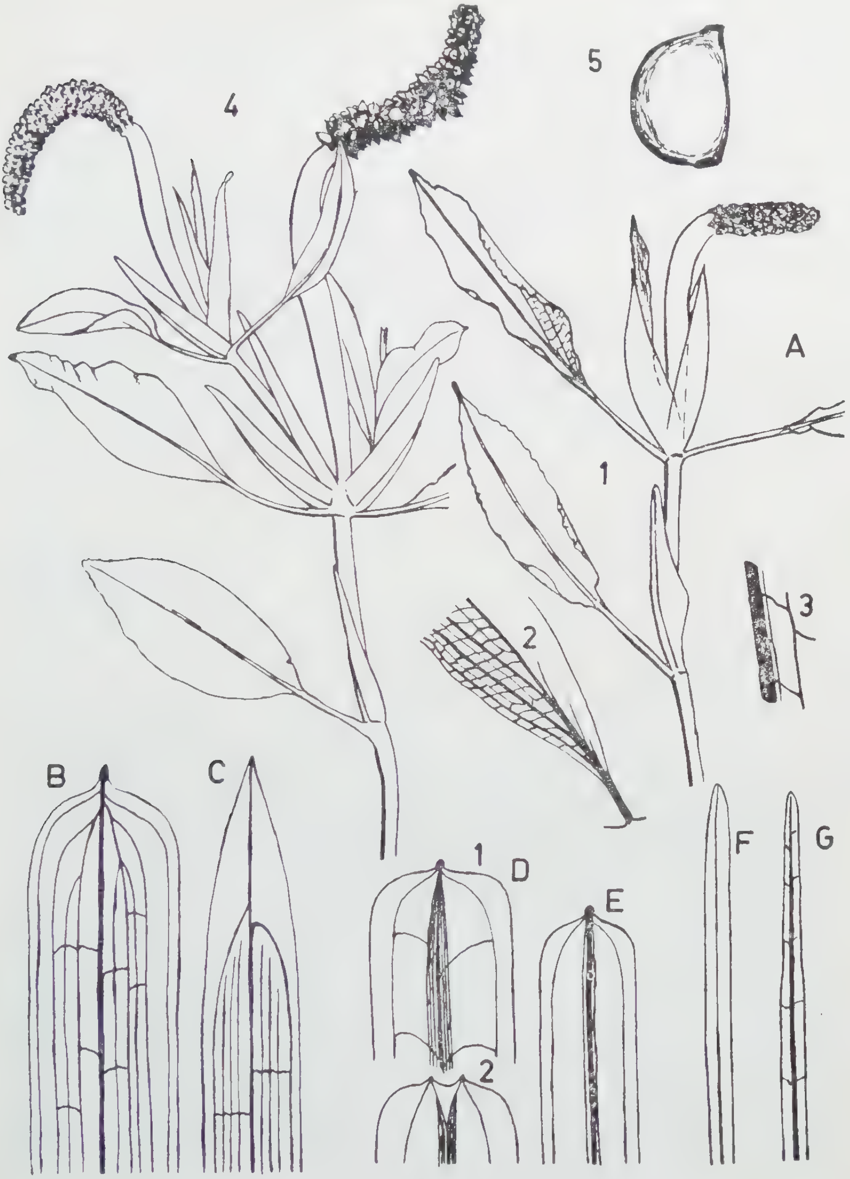


Figure 1. Potamogetones of the Zuidlaren Lake.

A = *P. zizii* M. et K. 1. shoot with a peduncle and ear (1-8-1950); 2. lateral nerves on base of blade; 3. fine nerve along the mid-nerve; 4. shoot with a fruiting ear and a newly formed flowering ear (11-8-1950); 5. a mature fruit in fresh condition (3 mm high). The shoots $^5/_8$ of the full size.

Apices of blades from: B = *P. compressus* L. (wide 3 mm); C = *P. acutifolius* Link (2 mm); D = *P. obtusifolius* M. et K. (2 mm), 1. normal and 2. twotopped; E = *P. pusillus* L. var. *berchtoldi* A. subvar. *mucronatus* A. et G. forma *typicus* F. (2 mm); F = *P. pusillus* L. var. *tenuissimus* M. et K. subvar. *angustifolius* F. (0.5 mm); G = *P. pectinatus* L. var. *scoparius* W. (0.5 mm).

However, the two dark knobs, which are said to occur usually at the bases of the leaves, are not present in my specimens.

I found this species only in a peat-ditch about 5 km S of the Lake.

15. **P. obtusifolius** Mertens & Koch.

Characterized by somewhat flattened stems and short peduncles. Leaves about 3 mm wide, very blunt tops, while end of mid-nerve protrudes as a very small point only, fig. 1 D 1; I found one leaf with a branched mid-nerve and consequently two small points, fig. 1 D 2.

The plants grow very profusely in pools of open water amidst the *Scirpeto- Phragmitetum*. In some places they lie in very compact masses under water close on the mud. In other places they reach the surface and the uppermost leaves float on the surface. These floating leaves show a fatty lustre and after being dried a reddish colour.

16. **P. mucronatus** Schrad.

Formerly I have mentioned this species (Clason, 1928, II, p. 44). As I visited in 1950 several times the same place where it should be abundant according to my notes of 1928, and could not find it again, I am compelled to consider the occurrence of this species as uncertain.

17. **P. pusillus** L.

The plants of this species, characterized by round stems and fairly long peduncles, belong to two forms, *viz.* a variety with flat leaves and a variety with fine threadlike leaves. They correspond satisfactorily with the descriptions of the following two varieties.

a. var. *berchtoldi* Ascherson subvar. *mucronatus* Ascherson & Graebner. Width of leaves usually almost 2 mm. At some distance from the mid-nerve on both sides one parallel nerve in the parenchyma, in addition one nerve along each margin. Apex of leaf rounded with a small point, fig. 1 E. Peduncles about 25 mm long, that is often four times as long as the ear. Fruits about 1.5 mm high, often some knobs.

b. var. *tenuissimus* Mertens & Koch subvar. *angustifolius* Fischer. Habit threadlike, with at first sight only small differences between stems and leaves. Usually the internodes about 30 mm long carry leaves about 20 mm long. Apex of leaf runs down over a length of some mm and ends fairly abruptly in a conical, blunt point, fig. 1 F. Transverse section of leaf almost circular (diam. about 0.5 mm) with a very fine furrow on the upper-side; section shows one nerve only.

Both varieties occur among *P. obtusifolius*, *P. compressus* and other demerse waterplants.

20. **P. pectinatus** L. var. **scoparius** Wallraven.

Fresh rhizomes only 3 mm thick, vertical shoots hardly 50 cm long and usually not reaching the water-surface. Stems thin, at the base internodes 3 cm, upwards gradually shorter with increasing ramification. Leaves to 6 cm long with a tightly fitting, inconspicuous sheath around the stem. Apex ends fairly abrubtly in a blunt point, fig. G. Transverse section of leaf shows a flat upper-side and a semi-circular under-side, with two air-canals separated by a vertical septum, containing the mid-nerve. No marginal nerves; some rows of somewhat longish cells in the margins cannot be considered as nerves in my opinion. Greatest diam. 0.5 mm. Long peduncles (to 8 cm). Ears with separated whirls of fruits; large fruit-ears look out of proportion with the thin plants.

Scattered on the shallow sandy bottom of the eastern side of the Lake. There also *Alisma gramineum* Gmel., *Ceratophyllum demersum* L., *Myriophyllum spicatum* L., *Ranunculus circinnatus* Sibth., *Elodea canadensis* Rich., *Chara* sp. and *Tolypella* sp.

I found repeatedly more robust forms of this species adrift in the Lake. As I could not find rooted plants, I am satisfied that these plants were carried there by the water of the Hunze, a canalized river which debouches into the Lake from the South.

DISCUSSION

Of the 22 western-european species according to Ascherson and Graebner (l.c.), 19 were found in the Netherlands (Kloos, l.c.); recently *P. fluitans* was found by Kern and Reichgelt, 1950, p. 250), only *P. nitens*, *P. rutilus* and *P. filiformis* are not yet on record (table I). Of the Zuidlaren Lake and adjacent waters 14 species have been mentioned, however, only from 10 species herbarium-specimens are available.

P. perfoliatus and *P. lucens* show gradual variation of habit and especially of leaf-form, which is correlated obviously with the external circumstances. *P. pectinatus* also shows some variation, but the plants of the other species are strikingly alike and accord clearly to only one of the many forms described by Ascherson and Graebner (l.c.). Only *P. pusillus* shows two forms, but the plants of each form are also strikingly alike.

Kloos (l.c., p. 556) encountered among extensive herbarium-material from the Netherlands only two specimens, which he suspected to be hybrids of two species. I did my utmost to find hybrids, but I did not succeed. As in several habitats of the Lake-area plants of different species grow interwoven, one should expect hybridisation as there were many hybrids mentioned in literature.

REFERENCES

Ascherson, P. and P. Graebner, Synopsis der Mitteleuropäischen Flora. — Leipzig, 1913, Bnd I, p. 455—548.

Clason, E. W., De plantengroei van het Zuidlaarder Meer en omgeving. — De Levende Natuur, 1928, II, p. 40—45.

Havinga, B., Studiën over flora en fauna van het Zuidlaarder Meer. — Diss. Groningen, 1919.

Heimans, E., H. W. Heinsius and Jac. P. Thysse, Geïllustreerde Flora van Nederland, 17th ed. by J. Heimans, A. W. Kloos and G. Kruseman. — Amsterdam, 1950.

Kern, J. and Th. Reichgelt, Over enige critische planten van onze flora. — Ned. Kruidk. Arch., 1950, dl. 57, p. 244—261.

Kloos, A. W., Het geslacht Potamogeton L. in Nederland. — Ned. Kruidk. Arch., 1936, dl. 46, p. 525—576.

Vuyck, L., Revisie van het geslacht Potamogeton. — Ned. Kruidk. Arch., 1895, 2de serie, dl. 6, p. 629—698.

OBJECTIVE COMBINATIONS OF SPECIES*

BY

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(Reveiced October, 1952)

In our research of Dutch grasslands, those are characterized in different ways. This is done to avoid partiality, and became possible because more than one method of botanical analysis has been applied. Namely, the productivity method or dry weight analysis (*4*, *6*, *8*, *13*), in some cases replaced by estimation of the weight proportions of the species, as well as the 25 cm² specific frequency (= frequency of occurrence — valency) method, combined with the order- or rank method (*2*, *4*, *5*, *8*) are used, while in many cases also completing lists of species of the concerning fields are made.

To begin with, the grasslands could be distinguished according to those species which were leading in weight proportion. For these so called dominance communities must be referred to *1*, *3*, *11* and *12*.

In the second place, a characterization of agricultural importance has been worked out, for which the 25 cm² (specific) frequency percentages are used instead of weight percentages, because their variability is smaller, and real dominancy is replaced by potential dominancy. With this system of combinations of frequent species, preference has been given to species of extreme agricultural value, good as well as bad ones. See a.o. *7* and *9*.

In the third place has been tried to place the examined grasslands in the system of BRAUN–BLANQUET. The real significance of this sociological system lies more in the indicating value of combinations of species than in the distinction of characteristic species. It is a pity that the generally used method of this School is rather subjective. It is remarkable that this pure scientific sociological School still sticks to the choosing of the so called typical places for the readings, while with the applied botanical grassland research already during a considerable time objective methods of sampling are used. The agricultural science wants reliable average values. The work of the School of BRAUN–BLANQUET would win a great deal in importance if one would endeavour to examine homogeneous vegetations with the aid of a (specific) frequency method. A test of the grassland-associations is being worked out by us, using the numerous analyses, acquired in an objective way. For this, the combination of the species is put in the first place, then afterwards it will appear how far we can speak of faithfulness by comparing the presence- and (specific) frequency percentages of the separate species in the different associations.

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* Summary of a paper, read on the 27th Dutch Day for Biosociology and Palaeobotany at Utrecht, April 29, 1951.

In the fourth place, finally, it seemed desirable to divide the grasslands according to combinations of frequent species, for which no preference is given to species which are significant in agricultural view, as in our characterization mentioned before in the second place. This new characterization is especially of ecological importance, because it appeared that combinations as well as frequencies of species have indicating value (*10*, *12*). To see which species really occur together or avoid each other, a mathematical statistical working out of the data of the first thousand of grasslands which have been analysed with the specific frequency method, is being done by Miss J. P. Baretta. Correlations (r-values) between two species, every time, are being calculated, not according to the orthodox method but with formulae of the agricultural mathematician Dr G. Hamming (Wageningen). For this, not only the number of cases, both species occur together or each separately (yes or not above certain specific frequency limits which are determined according to the most likely spreading of the F %'s), but also the number of cases, none of them is present, are taken account of. $R = 0$ means that the species are found together as many times as agrees with the degree of their respective occurrence, while $+1$ or -1 means that they occur always, respectively never, together.

Figure 1 indicates the constellation of grasslandplants which must be found in at least 30 parcels, will the reliability be satisfactory. The distances between the abbreviations of the species are about proportionate to the sizes of the positive r-values. The colour of the communicating lines indicates the correlation class, e.g. red means the highest class, from 0.70 — 1. The map shows that the constellation must properly be thought ball-shaped. Certain groups of species which have a great correlation with each other, as those of *Molinia coerulea* Moench. — *Sieglingia decumbens* Bernh. — *Potentilla erecta* Räuschel — *Carex panicea* L. — *Cirsium dissectum* Hill.; *Arrhenatherum elatior* J. et C. Presl. — *Trisetum flavescens* P. B. — *Dactylis glomerata* L; *Anthoxanthum odoratum* L. — *Rumex acetosa* L. — *Holcus lanatus* L.; *Caltha palustris* L. — *Lychnis flos-cuculi* L. — *Glyceria maxima* Holmb.; *Lolium perenne* L. — *Cynosurus cristatus* L. — *Trifolium repens* L.; *Ranunculus repens* L. — *Alopecurus geniculatus* L. — *Glyceria fluitans* R. Br. are obvious to the eye. In these objective combinations of frequent species, associations of the Swiss-French School can often be recognized. They are tested herewith for their justness. For instance, the fact that *Phleum pratense* L. and *Cynosurus cristatus* L. are both correlated with *Lolium perenne* L. and *Trifolium repens* L., but not positively correlated with each other, pleads in favour of a division of the *Lolieto–Cynosuretum* into a fat and a poor form. By doing justice to the occurrence together, as well as to the mass, a real bridge is built between the Southern and the Northern Sociological Schools.

It probably will be possible to calculate the correlation between

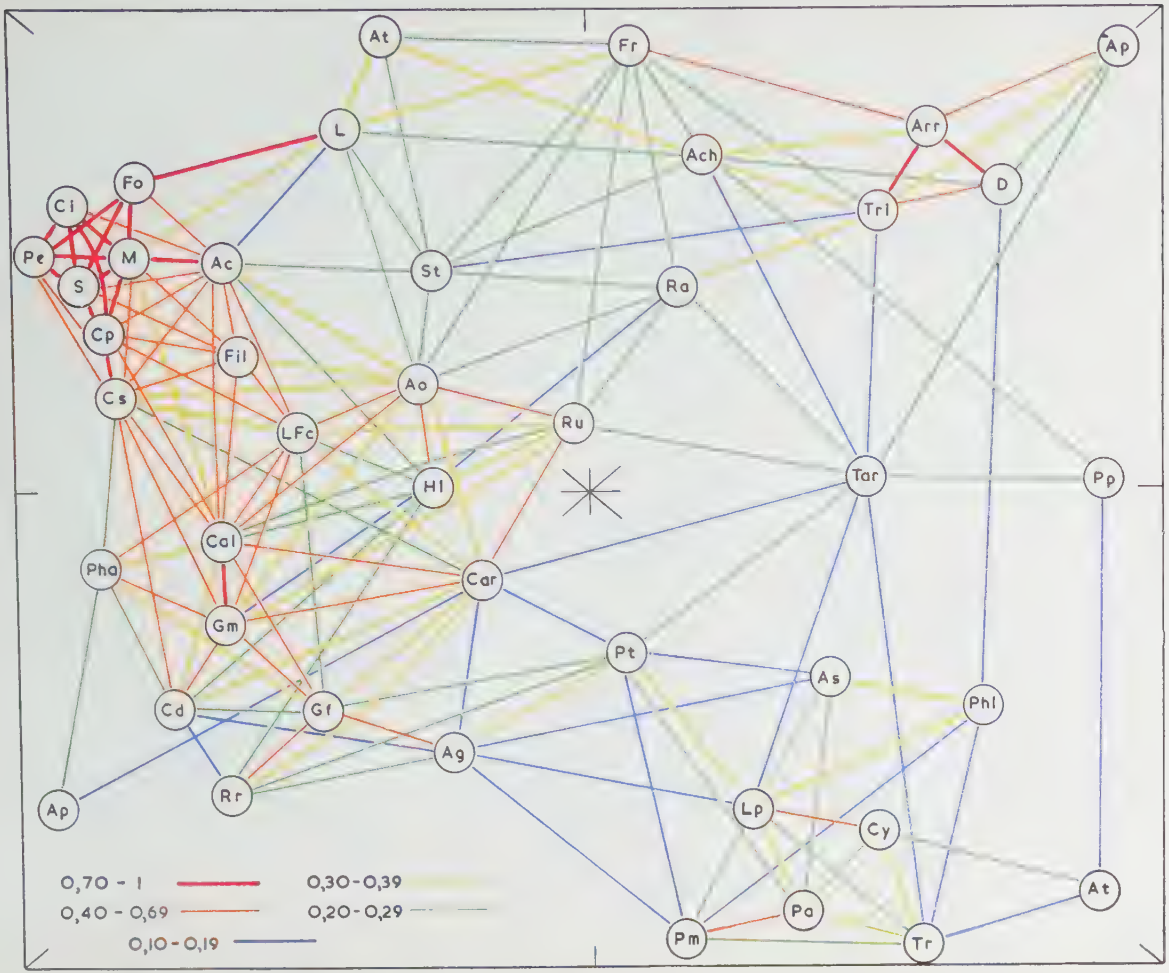

Fig. 1. Preliminary constellation of herbage plants. Correlation classes in colours: 0.70–1 red; 0.40–0.69 orange; 0.30–0.39 yellow; 0.20–0.29 green; 0.10–0.19 blue.

ABBREVIATIONS

Ac	Agrostis canina
Ach	Achillea millefolium
Ag	Alopecurus geniculatus
Ao	Anthoxanthum odoratum
Ap	Alopecurus pratensis
Arr	Arrhenatherum elatius
As	Agrostis stolonifera
At	Agrostis tenuis
Cal	Caltha palustris
Car	Cardamine pratensis
Cd	Carex disticha
Ci	Cirsium dissectum
Cp	Carex panicea
Cs	Carex stolonifera
Cy	Cynosurus cristatus
D	Dactylis glomerata
Fil	Filipendula ulmaria
Fo	Festuca ovina
Fr	Festuca rubra
Gf	Glyceria fluitans
Gm	Glyceria maxima
Hl	Holcus lanatus
L	Luzula campestris
LFc	Lychnis flos-cuculi
Lp	Lolium perenne
M	Molinia coerulea
Pa	Poa annua
Pe	Potentilla erecta
Pha	Phalaris arundinacea
Phl	Phleum pratense
Pm	Plantago major
Pp	Poa pratensis
Pt	Poa trivialis
Ra	Ranunculus acer
Rr	Ranunculus repens
Ru	Rumex acetosa
S	Sieglingia decumbens
St	Stellaria graminea
Tar	Taraxacum officinale
Tr	Trifolium pratense
Tri	Trisetum flavescens

groups of species, using the r-values of all couples of species. Herewith the existence of combinations of plants would be proved in a mathematical way.

Finally it seems that, by drawing four heartlines in the constellation figure, the species are divided respectively into those of hay fields (above) or pastures (below), into dry (right-above) or moist (left-below), fertile (right-below) or poor (left-above) soils, and into acid- (left) or lime loving (right) plants. This drawing which has been composed only with the aid of mathematical statistical data, demonstrates herewith already immediately its ecological sense.

REFERENCES

1. Ennik, G. C. et D. M. de Vries (1950), *Waardering en oecologie van dominantiegezelschappen.* Versl. Centr. Inst. Landbouwk. Onderz. 1949, p. 15–17, Wageningen.
2. Nielen, G. C. J. F. et J. G. P. Dirven (1950), *De nauwkeurigheid van de plantensociologische 1/4 dm² frequentie-methode.* (Summary: *The accuracy of the 25 cm² specific frequency method.*) Versl. Landbouwk. Onderz., 56, 13, p. 1–27, 's Gravenhage.
3. Sanders, M. et M. L. 't Hart (1951), *Droge-stofopbrengsten van de meest voorkomende dominantie-gezelschappen.* (Summary: *Dry-weight yields of the most frequent dominance societies.*) Versl. Centr. Inst. Landbouwk. Onderz. 1950, p. 24–26, Wageningen.
4. Vries, D. M. de (1937), *Methods of determining the botanical composition of hayfields and pastures.* Rep. Fourth Intern. Grassl. Congr., Great Britain, p. 474–480, Aberystwyth.
5. Vries, D. M. de (1938), *The plant sociological combined specific frequency and order method.* Chron. Bot., 4, 2, p. 115–117. Leiden.
6. Vries, D. M. de (1940), *De drooggewichtsanalytische methode van botanisch graslandonderzoek voor beweid land.* (Summary: *Die botanische Trockengewichtsanalyse für Weiden.*) Versl. Landbouwk. Onderz., 46, 1, A, p. 1–19, 's Gravenhage.
7. Vries, D. M. de (1948), *Method and survey of the characterization of Dutch grasslands.* Vegetatio, Acta Geobot., 1, 1, p. 51–57. The Hague.
8. Vries, D. M. de (1949), *Survey of methods of botanical analysis of grassland.* Rep. Fifth Intern. Grassl. Congr., Netherlands, p. 143–148. The Hague.
9. Vries, D. M. de (1950), *Graslandtypen en hun oecologie.* Ned. Kruidk. Arch., 57, p. 28–31, Amsterdam.
10. Vries, D. M. de (1951), *Voortgang en nieuwe aspecten van het type-onderzoek.* (Summary: *Progress and new aspects of the type-research.*) Versl. Centr. Inst. Landbouwk. Onderz. 1950, p. 18–22, Wageningen.
11. Vries, D. M. de et Th. A. de Boer (1943), *Korte mededeling over de plantkundige samenstelling en waardering van het grasland der kleine boerenbedrijven.* Landbouwk. Tijdschr., 55, 679, p. 433–438, Wageningen.
12. Vries, D. M. de et G. C. Ennik (1952), *Dominance and dominance communities.* Acta Bot. Neerl., 1, xxx, p. xxx–xxx, Amsterdam.
13. Zijlstra, K. (1940), *Over de botanische samenstelling van grasland. Bepaling van de gewichtspercentages der plantensoorten.* (With summary in German.) Versl. Landbouwk. Onderz., 46, 7, A, p. 343–377, 's Gravenhage.

DOMINANCY AND DOMINANCE COMMUNITIES*

BY

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Dominancy of a species is to be considered as an expression of the success, the species has in the struggle for life, and as the concurrence may be taken as the essential plant sociological factor, the dominancy must, from a theoretical point of view, be of great importance for this branche of science.

Now the case is that dominancy shows itself in different respects. In the first place the predominating, tallest plants determine for the greater part the appearance and the rough composition of the botanical landscape. In the second place, the often mosaiclike variance of dominants forms the more detailed structure of the plantcover. In the third place, the mass working of predominating species changes the original habitat in the long run more or less. Clear examples of this are the succession in silting up, in forming of dunes and of land by water- and marshplants. In the fourth place dominancy of a species indicates special characteristics of the habitat.

Up till now the ecological significance of dominancy was, though for good reasons, only supposed. With the aid of the results of our analyses of the herbage and the habitat of 855 Dutch grasslands the latter could also be proved now. The botanical composition of these grasslands was studied by using the 25 cm² specific frequency (= frequency of occurrence) method (2, 3, 4) and the dry weight analysis (= productivity method) (3, 5, 10). The environmental factors, noted or analysed, were a.o. use of the land, degree of humidity, percentages of humus, sand (fine and coarse) and clay, phosphate- and potash status and pH-water of the soil.

It is shown that the more frequently a species occurs the more evident its coherence with special environmental factors demonstrates itself. This, however, does not avail for every species regarding every habitat factor, but only for those species which are *frequency indicator* for special factors. Exceptions are the few species, called by us *presence indicators* which only need to be present in a small quantity to give good indications concerning an environmental factor, and further those species which even at a high frequency have not any indicating value for this factor. A good example of the latter group is *Festuca*

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* Summary of a paper, read on the 26th Dutch Day for Biosociology and Palaeobotany at Utrecht, 19 November 1950.

rubra L. which grass can be as frequent at a pH 4 as at a pH 8. (It seems that the tuftforming strain of this species is strongly acidloving in contrast with the strain with rhizomes which is moderately limeloving.)

Now, for instance, it generally appears to be true that for frequency indicators the spreading (standard deviation) around the mean pH becomes smaller at higher 25 cm² frequencies (of occurrence) and higher weight percentages. Moreover with acido-frequent species (e.g. *Agrostis canina* L. and *Anthoxanthum odoratum* L. (Fig. 1)) the mean pH changes to the acid side with increasing frequency, but with basifrequent species as *Dactylis glomerata* L. (Fig. 2 and 3) and *Trifolium fragiferum* L. (8: Fig. 2) it changes to the basic side (see Tables 1 and 2). This change can be explained by the unequal distribution of the grasslands over the different pH classes and the already mentioned grouping around the mean pH, when they appear more in mass.

Presence indicators behave in a different way. They react so strongly on the environmental factor, for which they are presence indicator, that they show in low frequencies an equally small spreading

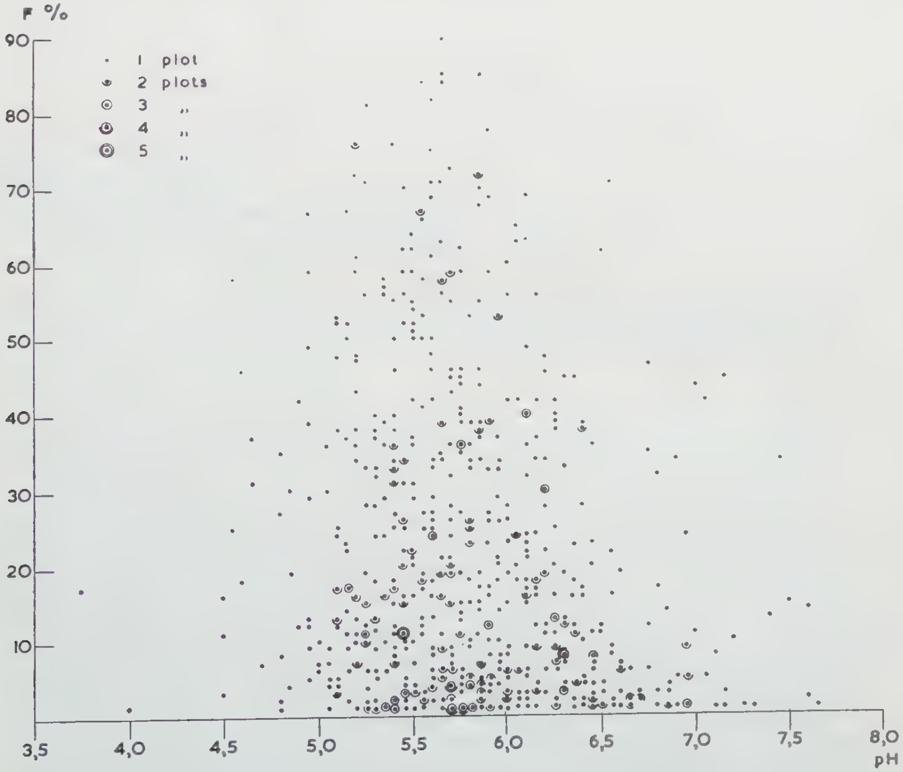

Fig. 1. Relation between the 25 cm² frequency of occurrence (F %) of *Anthoxanthum odoratum* L. and the pH-water of the soil.

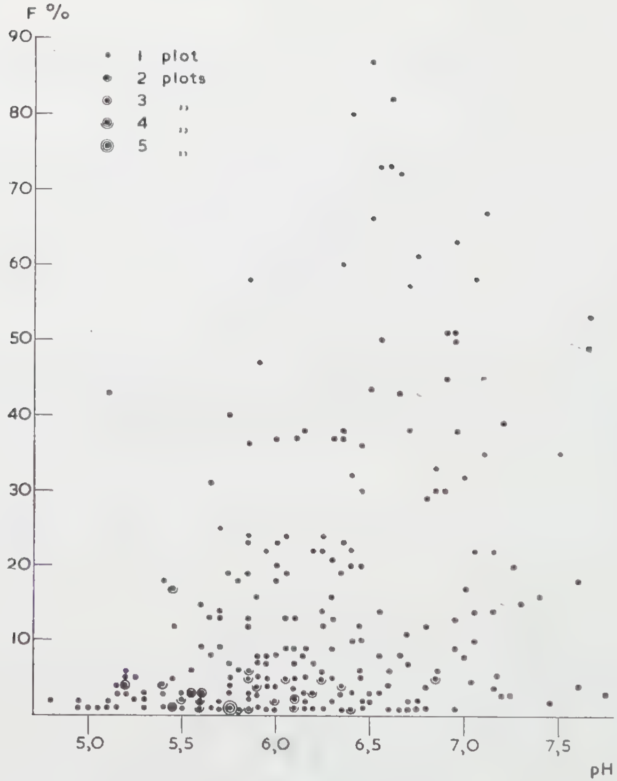

Fig. 2. Relation between the 25 cm² frequency of occurrence (F %) of *Dactylis glomerata* L. and the pH-water of the soil.

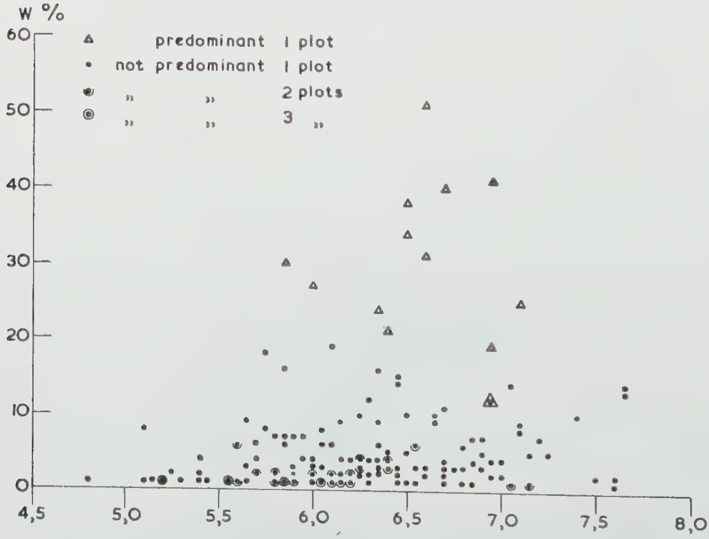

Fig. 3. Relation between the dry weight percentage (W %) of *Dactylis glomerata* L. and the pH-water of the soil.

TABLE 1

Mean pH and standard deviation (σ) of *Anthoxanthum odoratum* L. and *Dactylis glomerata* L. at different frequency (F) classes.

	Anthoxanthum odoratum			*Dactylis glomerata*		
F %	Mean pH	σ	Number of plots	Mean pH	σ	Number of plots
1—10	5.9	0.59	264	6.0	0.58	172
11—25	5.8	0.55	184	6.3	0.56	52
26—50	5.7	0.49	153	6.6	0.56	31
> 50	5.6	0.33	73	6.7	0.39	17

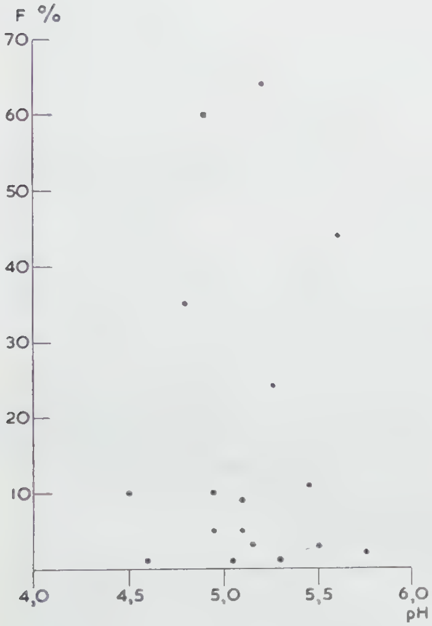

Fig. 4. Relation between the 25 cm^2 frequency of occurrence of *Nardus stricta* L. and the pH-water of the soil.

around the mean value of the concerning habitat factor as in high frequencies. So for these species, there does not occur a changing of the mean pH in acid- or basic direction at higher frequencies. Examples of real presence indicators are up till now: *Nardus stricta* L. (Fig. 4) for acid soils (pH-water 4.5—5.8) and *Festuca ovina* L. (8: Fig. 1) for an insufficient phosphate status. Of this, the number of data is relatively small and it is not impossible that in extending this number, *Nardus* will appear to behave, regarding the pH, more as a frequency- than as a presence indicator. All this only concerns separate habitat factors and so it is an open question if exclusive characteristic species (School of BRAUN-BLANQUET), essentially being the same as the presence indicators for the habitat as a whole, even occur in grassland. Therefore all or nearly all characteristic species would be selective or preferential, at least in the grassland formation.

After this illustration of the importance of dominancy, particularly from an ecological point of view, we will consider now the *dominance communities*. Apart from the fine mosaic-forming differences in predominancy, a sward often shows, in this research of the Dutch grasslands a dominance community is determined by the species which has the highest average dry weight percentage in the area sampled. If the weight part of the leading species amounts to at least 25 or 50 %, the dominance community is called pure and very pure respectively. If the weight percentage of the dominant is under 25 which often occurs or if two or more species form the leading part, we speak of an impure and mixed community respectively. The facts, published already before (6, 7, 9), that dominancy can change temporarily under influence of the season, or by influences of weather conditions as drought or severe frost, are a great prejudice for the characterization by the predominating species, but do not change much of the indicating value of predominancy.

In the paper about the valuation and ecology of dominance communities (1) are given in Table 1 the lowest, mean and highest grades of quality of the sward for the principal dominance communities and in Table 2 the preference of those communities for distinct degrees of the most important environmental factors (use, humidity, clay-humus percentage, type of soil, pH, phosphate- and potash condition). The agricultural valuation of the relative dominance communities is decreasing in the following order (mean grades of quality between brackets): *Lolium perenne* (7.4), *Poa trivialis* (6.4), *Cynosurus cristatus* (6.3), *Dactylis glomerata* (6.2), *Poa pratensis* (6.1), *Trifolium repens* (6.0), *Alopecurus pratensis* (6.0), *Festuca pratensis* (5.9), *Agrostis stolonifera* (5.8), *Holcus lanatus* (5.1), *Agrostis tenuis* (5.0),

TABLE 2

Mean pH and standard deviation (σ) of *Dactylis glomerata* L., either predominant in weight or not.

Dactylis glomerata	Mean pH	σ	Number of plots
Not predominant	6.3	0.59	146
Predominant	6.6	0.36	13

TABLE 3

Dry weight yields of dominance communities in different years, expressed in percentages of the year average of all grasslands of which the yield is determined. Number of botanical analyses between brackets.

Dominance community	1946	1947	1948	1949
Lolium perenne	114 (63)	102 (33)	99 (15)	107 (18)
Festuca pratensis	102 (15)	118 (3)	60 (1)	116 (2)
Poa trivialis	118 (6)	106 (2)	101 (1)	
Agrostis stolonifera	96 (20)	96 (25)	89 (1)	95 (8)
Festuca rubra	92 (12)	74 (3)	87 (6)	98 (5)

Festuca rubra (4.6), *Deschampsia caespitosa* (3.8), *Agrostis canina* (2.9), and *Molinia coerulea* (1.9). With regard to the synecology, it appears a.o. that the *Poa trivialis*-community generally occurs at a better P-status than the community of *Lolium perenne*, while this is just the contrary with the potash status. The latter community is also in a high degree bound to neither too moist, nor too dry a situation of the soil and is especially found on pure pastures (only grazed grasslands).

To complete, Table 3 gives the dry weight yields of the herbage of the most occurring dominance communities for the years 1946, 1947, 1948 and 1949, expressed in percentages of the year average of all grasslands of the yield research of M.L. 'T HART (Wageningen), including those of which no botanical analysis has been made. In agricultural view, it is of importance that for certain communities (e.g. those of *Poa trivialis*, *Lolium perenne* and *Festuca pratensis*) the yields generally lie higher than the average yield, and for others, e.g. those of *Agrostis stolonifera* and *Festuca rubra*, the yields lie below that mean yield. In proportion to the weight amount of the predominant species being higher, this is more pronounced.

REFERENCES

1. ENNIK, G. C. et D. M. DE VRIES (1950), *Waardering en oecologie van dominantiegezelschappen.* Versl. Centr. Inst. Landbouwk. Onderz. 1949, p. 15—17, Wageningen.
2. NIELEN, G. C. J. F. et J. G. P. DIRVEN (1950), *De nauwkeurigheid van de plantensociologische $\frac{1}{4}$ dm^2 frequentie-methode.* (Summary: *The accuracy of the* 25 *cm*^{2} *specific frequency method.*) Versl. Landbouwk. Onderz., 56, 13, p. 1—27, 's-Gravenhage.
3. VRIES, D. M. DE (1937), *Methods of determining the botanical composition of hayfields and pastures.* Rep. Fourth Intern. Grassl. Congr., Great-Britain, p. 474—480, Aberystwyth.
4. VRIES, D. M. DE (1938), *The plant sociological combined specific frequency and order method.* Chron. Bot., 4, 2, p. 115—117, Leiden.
5. VRIES, D. M. DE (1940), *De drooggewichtsanalytische methode van botanisch graslandonderzoek voor beweid land.* (Summary: *Die botanische Trockengewichtsanalyse für Weiden.*) Versl. Landbouwk. Onderz., 46, 1, A, p. 1—19, 's-Gravenhage.
6. VRIES, D. M. DE (1942), *Over de invloed van jaargetijde en weer op de botanische samenstelling van grasland.* Ned. Kruidk. Arch., 52, p. 303—307, Amsterdam.
7. VRIES, D. M. DE (1943), *Grasland en weersgesteldheid.* (Summary: *Grassland and Weather.*) Landbouwk. Tijdschr., 55, 676, p. 268—274, Wageningen.
8. VRIES, D. M. DE (1951), *Voortgang en nieuwe aspecten van het type-onderzoek.* (Summary: *Progress and new aspects of the type-research.*) Versl. Centr. Inst. Landbouwk. Onderz. 1950, p. 18—22, Wageningen.
9. VRIES, D. M. DE et J. KOOPMANS (1948), *De botanische samenstelling van Nederlandse graslanden. II. De invloed van het jaargetijde op de botanische samenstelling van grasland.* (Summary: *About the seasonal influences on the botanical composition of the sward.*) Versl. Landbouwk. Onderz., 54, 6, p. 1—14, 's-Gravenhage.
10. ZIJLSTRA, K. (1940), *Over de botanische samenstelling van grasland. Bepaling van de gewichtspercentages der plantensoorten.* (With summary in German.) Versl. Landbouwk. Onderz., 46, 7, A, p. 343—377, 's-Gravenhage.

ACTIVE UPTAKE, VACUOLE-SECRETION AND PLASMATIC TRANSPORT OF CHLORIDE-IONS IN LEAVES OF VALLISNERIA SPIRALIS

BY

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(*Received Nov. 1st 1952*)

Leaves of *Vallisneria* accumulate substances e.g. aminoacids and salts in their vacuoles. This appears from the increase of the osmotic value of the vacuole sap. The accumulation of chloride and phosphate ions depends on the intensity of the illumination to which the leaves are exposed. We have termed this process photoaccumulation and found that it does not depend on the presence of carbon dioxide. The leaves absorb the salts as well from a solution as from a 2 % agar gel. We confine ourselves here to the process of uptake of chloride-ions and use the method of uptake from agar strips because it provides the opportunity to localize the uptake in a definite part of the leaf. The rest of the leaf gets the chloride-ions by means of transport from the absorbing part. So we have an absorbing and a transport zone. The length of the leaves used was mostly 7.5 cms, the absorbing zone being 2.5 cms and the free part of the leaf 5 cms. 2.5 cm leaf lengths were analysed before and after the uptake. The methods used have been described in a preceding paper (Arisz 1947). A survey of the results of the translocation experiments formerly obtained will be given here with the aid of figs. 1–4. Fig. 1 gives the results

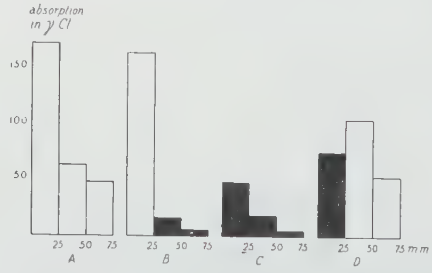


Fig. 1. Influence of exposure to light on uptake and transport of chloride in leaves of *Vallisneria.* In A the whole leaf is in the light, in B only the first zone. In C the whole leaf is in the dark, in D the first zone in the dark and the free part in the light. The first zone of 25 mms is 24 hours in contact with a solution of 0.01 mol KCl + $CaSO_4$ in 2 % agar. The second and third zone are free in moist air on wet filterpaper. On the ordinate the increase in Cl-content; temp. 25° C. Pretreatment during 24 hours in aerated distilled water in the light. (From Arisz 1947). In this and the following figures on the ordinate the amount of the uptake in γ Cl.

of 4 different ways of exposure to light. In A the whole leaf is exposed to the light, in B only the absorbing zone, in C the whole leaf is in the dark, in D the absorbing zone is in the dark and the free part in the light. The first 2.5 cm zone, the absorbing zone, is in contact with a solution of 0.01 M KCl in 2 % agar with an addition of $CaSO_4$. The second and third zones forming the free part are in moist air on wet filter paper. A series of 8 leaves is put in a closed glass box the bottom of which was covered with water. In fig. 1A (whole leaf in the light) there is a strong accumulation in the absorption zone and a slight translocation to the free part. In 1B (free part of the leaf in the dark) this translocation is still slighter. In 1C (whole leaf in the dark) both uptake and transport are slight. Only in 1D there is a remarkable translocation of chloride from the absorbing zone, which is in the dark, to the free part of the leaf, which is in the light (Confer fig. 2).

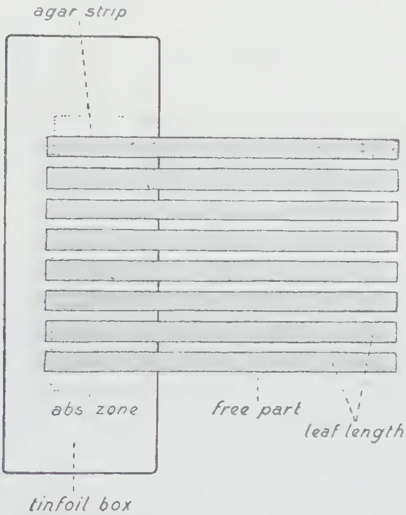


Fig. 2. 8 leaf lengths are with their absorptionzone between agar plates in a tinfoil box, which is closed during the experiment. The free parts of the leaf lengths protrude through perforations in the side wall of the box.

The pretreatment of the leaves after cutting has an important influence on the power of the plant for uptake and transport. This is elucidated by fig. 3. In A the leaves are directly used after cutting;

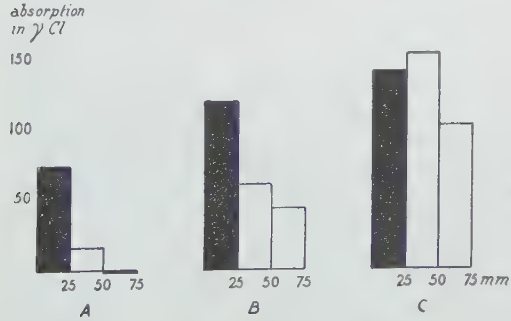


Fig. 3. Influence of the pretreatment on the transport of chloride. Exposure as in Fig. 1D:A, no pretreatment, B, 16 hours and C, 24 hours pretreatment in distilled water. In C a strong transport to the free part of the leaves. (From ARISZ 1947).

in B there is a pretreatment of 16 hours in distilled water in the light and in C the pretreatment lasts 24 hours. Only after 24 hours pretreatment the translocation effect of fig. 1D is obtained. This is indicative of the strong influence of cutting on the condition of the leaves and points to the activity of the protoplasm in translocation.

As a result of these experiments the conditions are known which favour translocation of chloride ions. The absorbing zone has to remain in darkness which brings about a small accumulation in this zone and the free part has to be exposed to light in order to promote the photoaccumulation of transported chloride ions in these parts.

To explain these phenomena two schemes were considered (Arisz III 1948) which we have reproduced in fig. 4. The schemes represent the two parts of the leaf, the absorbing zone and the free part, by two cells A and B. In Scheme I the accumulating mechanism is situated near the outer boundary of the cytoplasm and the tonoplast is assumed to be permeable to the chloride ions. In Scheme II the accumulating mechanism is situated near the inner boundary of the cytoplasm, the tonoplast and the ions of the medium having free entrance into the cytoplasm. According to scheme I the chloride ions are accumulated in the plasm and the vacuole. Translocation in the plasm of absorbed chloride ions from cell to cell is only possible if there are plasmodesms which connect the cytoplasm of adjacent cells. Evidently there is also the possibility that the chloride ions are translocated outside the plasm through the cell walls and that they are subsequently absorbed by the active accumulating mechanism of the cells in the free part. The transport of chloride ions from cell to cell through plasmodesms does not agree with the result obtained in Fig. 1D that the free part of the leaf can obtain more Cl ions than the absorbing zone itself. This is not in accordance with a diffusion

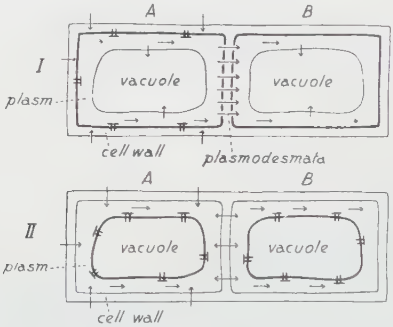


Fig. 4. The scheme represents the two parts of the leaf, the contactzone and the free part by two cells A and B. In scheme I the outer boundary of the protoplasm is supposed to be impermeable for Cl ions, and the tonoplast permeable. An active mechanism for the introduction of ions is situated in the outer layer of the plasm. By plasmatic connections between the two cells the substances invade cell B. Scheme II represents the condition that the outer layer of the plasm gives passage to Cl ions. The tonoplast is here impermeable and the accumulating mechanism is situated in the plasmatic layers bordering the vacuole. (From Arisz 1948)

process from cell to cell which requires that concentrations gradually decrease. This means that it is not the active process of uptake in the absorbing zone that determines how much chloride ions will be accumulated in the different parts of the leaves, but that this depends on the strength of the accumulation in the different parts of the leaf.

Though the assumption that the transport takes place in the cell-walls can give an interpretation of the different strengths of the accumulation in different parts of the leaf, it is not in accordance with our finding that particularly the transport is very sensitive to a wound stimulus, while the photoaccumulation process is less sensitive. This makes a mere translocation of the ions in the walls outside the protoplasm very unlikely.

Scheme II seems to give a reasonable interpretation of the results. Here the accumulation mechanism is situated near the border of the vacuole and takes the chloride ions from the cytoplasm into the vacuole. This process can be compared to a secretionprocess. The ions pass from one cell to an other either by plasmodesms or they diffuse through the transverse walls. When arrived in the cytoplasm of the cells of the free part they can be secreted into the vacuoles by the active accumulating process. It is in close agreement with this scheme that substances once secreted into the vacuoles remain there and do not diffuse to adjacent cells.

In the years after 1947 we have tried to extend and to corroborate the above mentioned experiments but the results were disappointing. The leaves used were less resistant and could not recover in 24 hours from the effect of cutting and wounding. In stead of an uptake by the darkened absorbing zone there was often a loss of salt owing to leakage. Besides it seemed desirable to take special precautions against a spreading of the transportsubstance over the surface of the leaves. This was obtained by coating the leaf between the region of absorption and the free part with a thin covering of vaseline. Experiments made in this way showed that such a spreading outside the cells was out of the question. Not until May 1952 could experiments be made with complete success. During May and June of this year the material remained in that specially good condition which is required for transport experiments, but after that it declined again.

Fig. 5 gives a translocation over a region of 12.5 cms in 24 hours.

In the meantime we managed to show that even leaves in a less satisfactory condition could be used for transport experiments if sugar or fructose was administered to the leaves. A conclusive proof of plasmatic transport can be given by the following experiment with a leaf having a darkened absorbing zone and the free part exposed to the light (fig. 6 and 7). The absorbing zone was put between two agar strips containing KCl and $CaSO_4$ in a tinfoil box. The free part of the leaf was exposed to light. The free parts of the series B and C were placed between two agarplates which contained 2 % fructose. In series B the agar strips with the absorbingzones also contained 2 % fructose. Between the absorbing zone and the free part of the leaf the surface of the leaf was covered with vaseline.

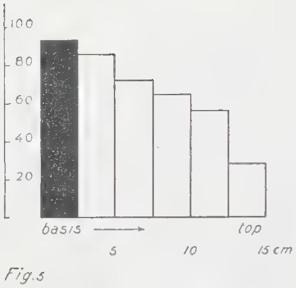
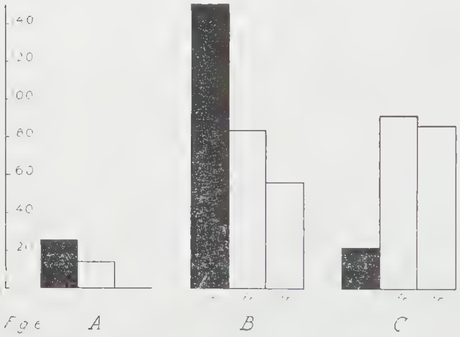
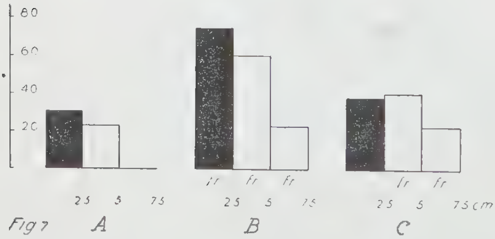


Fig. 5. Transport of chloride ions in leaf-lengths of 15 cm. The first zone of 2.5 cm, the absorbing part is in the dark. The rest of the leaf-length is exposed to light. 24 hours uptake from a solution of 0.01 M KCl + $CaSO_4$ in agar.



Figs 6 and 7. Influence of fructose on the transport of chloride ions in leaf-lengths of 7.5 cm. A, normal conditions; B, with addition of fructose to all the zones; C with addition of fructose only to the free part.

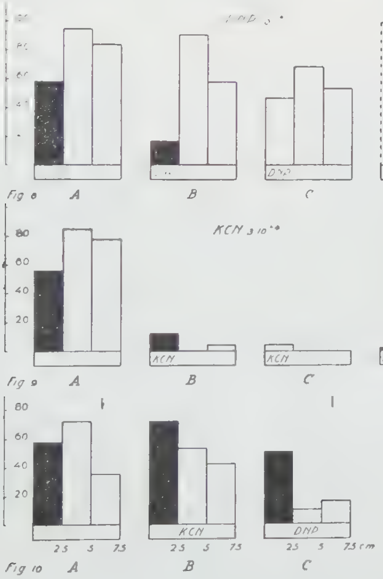


Without fructose the uptake and the translocation in all parts were slight. With fructose administered to all zones (series B) there is a strong accumulation of chloride in the absorbing zone and the translocation to the free part is considerable too. In C with fructose only administered to the free part the accumulation in the absorption zone is slight, but the transport to the free part is of the same strength. If one considers that these leaf lengths were lying between agar strips it will be clear that there can be no question of diffusion or spreading in the cell wall. The transport must be a vital process dependent on the presence of sugar and closely connected with metabolism. Such a transport can only take place in the cytoplasm.

The connection of translocation with metabolism can also be investigated in other ways. We analysed the transport in *Drosera* tentacles by means of substances which inhibit enzymatic processes. It is obvious that we can do the same with the processes in Vallisneria leaves. This research has only commenced but seeing the difficulty of getting sufficient material of the quality required for these experiments on transport it seems justified to communicate some preliminary results. They relate to the influence of 2–4 dinitrophenol and KCN on the uptake and transport of chloride ions.

All these experiments have been taken with the arrangement which had formerly given the most favourable conditions for transport i.e. after 24 hours' pretreatment in the light the absorbing zone is placed in the dark and the free part is exposed to the light. The duration of the experiments is always 24 hours at a temperature of 25° C.

In the first experiments the influence of 2–4, dinitrophenol (D.N.P.) on the uptake has been investigated (fig. 8B). It was added to the agar covering the absorbing zone. It gives a strong inhibition of the accumulation. But in the free part of the leaf there is a strong accumulation which proves that the transport is not checked by the inhibitor. As these substances must have passed the absorbing zone, it proves that D.N.P. even in the absorbing zone does not inhibit the uptake of substances into the cytoplasm. Accumulation in the absorb-



Figs 8, 9 and 10. Influence of inhibitors on the transport of chloride ions.

Fig. 8. In A and B the absorbingzone is in the dark and the free part is in the light. In C and D the whole leaf length is in the light. In B and C 2–4, Dinitrophenol 10^{-4} is administered to the absorbing zone.

Fig. 9. . In A and B the absorbingzone is in the dark and the free part is in the light. In C the whole leaf length is in the light. In B and C KCN 3.10^{-4} is administered to the absorbing zone. In D DNP is administered to the first zone and KCN to the second zone.

Fig. 10. In A, B and C the absorbing zone is in the dark and the free part in the light. In B KCN 3.10^{-4} and in C D.N.P. 10^{-4} is administered to the second zone.

ing zone being at the same time inhibited, it is obvious that the inhibited accumulating mechanism must be situated in the inner cytoplasm and that the accumulation is a secretion into the vacuole.

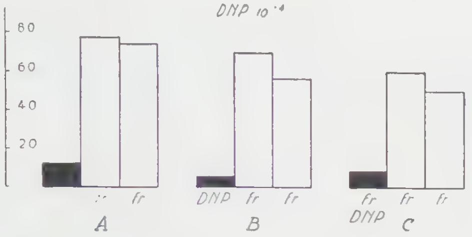
We have further traced the influence of D.N.P. when the whole leaf length was in the light. Fig.8D gives the result without D.N.P. Here the absorbing zone gets a high Cl content, that of the free part being much smaller. If D.N.P. is added to the agar covering the absorbing zone (fig. 8C) the accumulation in this zone is strongly decreased, but the translocation of chloride ions to the free part of the leaf is much larger as the competition of the mechanism which secretes ions into the vacuole of the cells of the absorbing zone is now ruled out. So, the result is approximately the same whether the absorbing zone to which D.N.P. is added is exposed to the light or stays in the dark.

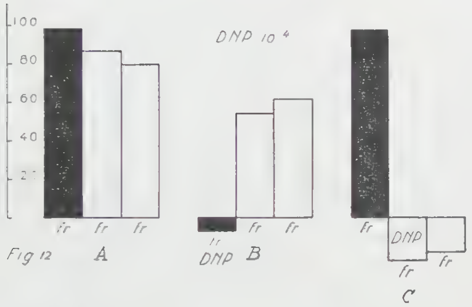
If KCN 3.10^{-4} is added to the absorbing zone a remarkable effect is produced (fig. 9). Now the accumulation in this zone as well as the translocation to the free part are strongly inhibited. Neither does it make any difference in this case whether the absorbing zone is in the light or in the dark (fig. 9 B and C, fig. 9C has to be compared with 8D).

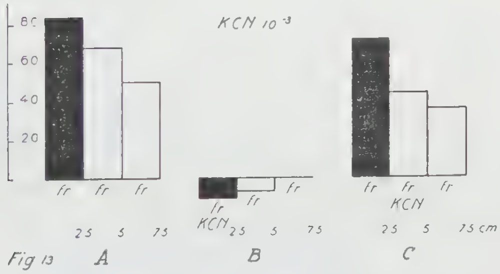
Three suppositions have to be considered to interpret this result: 1. KCN inhibits the translocation in the cytoplasm, 2. KCN inhibits the process of uptake at the outer boundary of the cytoplasm, 3. KCN has moreover an inhibiting influence on the process of vacuole secretion. Also a combination of these actions can be assumed.

By administering KCN to the free part of the leaf a possible influence on the transportprocess and on the secretion into the vacuole can be investigated. We have put the second zone of 2.5 cms between agar strips to which KCN 3.10^{-4} was added. The result is given in fig. 10B. It appears that KCN does not inhibit the secretion into the vacuole of the free part, neither has it an appreciable influence on the plasmatic transport. Fig. 9D corroborates this conclusion. Here dinitrophenol has been added to the first zone and KCN to the second one. D.N.P. inhibits only the secretion of Cl into the vacuoles of the first zone but does not interfere with the translocation to the free part. KCN has no effect if applied outside the absorbing zone. It seems therefore that KCN acts only on the uptake of chloride from the medium by the absorbing zone.

Once the substance has penetrated into the cytoplasm KCN neither inhibits its transport nor its accumulation in the vacuole. The difference in behaviour between D.N.P. and KCN with respect to the transport is also apparent from fig. 10B and C where the accumulation in the free zone is positively inhibited by D.N.P. KCN being without influence. The slighter translocation into the third zone can be ascribed to the less favourable condition of the material in this experiment. In later experiments D.N.P. was so harmful that the cytoplasm could scarcely endure its presence and often gave exosmosis of Cl.







Figs 11, 12 and 13. Influence of inhibitors on the transport of chloride ions. With addition of fructose.

Fig. 11. Influence of D.N.P. administered to the absorbing zone. Addition of fructose to the free part in A and B and to the entire leaf in C. The absorbing zone is in the dark and the free part in the light. In B and C Dinitrophenol is administered to the absorbing zone.

Fig. 12. Influence of D.N.P. administered in the first or the second zone. Addition of fructose to all parts of the leaf lengths. The absorbing zone is in the dark and the free part in the light. In B Dinitrophenol has been administered to the absorbing zone and in C to the second zone.

Fig. 13. Influence of KCN administered in the first or in the second zone on the transport of chloride ions. To all parts of the leaf lengths fructose has been supplied.

From figs 11, 12 and 13 it appears that even in the less favourable circumstances in October 1952 it was possible by addition of fructose to the different parts of the leaf to show the different effect of D.N.P. and KCN when administered either to the absorbing zone or to the free part of the leaf. So this is a conclusive proof that D.N.P. is an inhibitor specifically acting on the secretion of chloride ions into the vacuole. It does not inhibit the translocation in the cytoplasm nor the uptake through the outer cytoplasmic layer. KCN on the contrary acts particularly on the uptake in the cytoplasm and does not influence, or only in a slight degree, the accumulation in the vacuole and the translocation from cell to cell.

DISCUSSION

The experiments with inhibitors confirm and complete our former results. The view that substances are translocated in the living cytoplasm and are secreted from this plasm into the vacuoles agrees with our findings on the influence of Dinitrophenol. The inhibition of the translocation to the free part by administering KCN to the absorbing zone proves that this translocation is a process which takes place in the cytoplasm and not outside it in the cell walls. Spreading and diffusion outside the protoplasm cannot play a part in this transport process.

A new point is the influence of KCN on the uptake in the absorbing zone. We have formerly assumed that chloride ions easily penetrate into the cytoplasm. The inhibition of this uptake by KCN points to the presence of a metabolic system near or in the outer boundary of the cytoplasm which regulates the introduction of these ions into the cells. KCN has no influence or only a trifling one when it is administered to the transportzones. This indicates that the process which is sensitive to KCN is only connected with the uptake through the outer layer of the protoplasm. By inhibiting this process in the absorbing zone both uptake and transport are inhibited. As there is no chloride present in the cytoplasm the secretion in the vacuole also comes to a stand still.

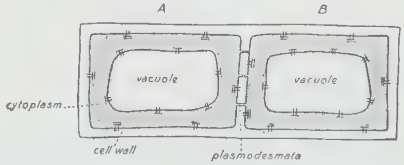


Fig. 14. Confer the schemes of fig. 4. There is an active accumulating mechanism situated near the outer boundary of the cytoplasm, which is inhibited by KCN and there is a second accumulating mechanism situated near the tonoplast, which secretes chloride ions into the vacuole. This process is inhibited by dinitrophenol. The transport takes place in the cytoplasm.

Fig. 14 gives the true scheme for the interpretation of these phenomena. There are two regulating mechanisms in the cytoplasm one at the outer boundary influenced by KCN and a second one at the inner boundary influenced by dinitrophenol. Transport is a vital process in the symplasm.

SUMMARY

The transport of chloride ions in the leaves of Vallisneria is a plasmatic process dependent on cell metabolism. It is checked by a wound stimulus and promoted by administering fructose.

Uptake from the medium is regulated by a process in the outer layer of the cytoplasm. KCN is an inhibitor of this process. There is an active secretion-process by which chloride ions from the cytoplasm are accumulated in the vacuoles. This process is inhibited by 2–4, dinitrophenol.

To Mrs H KNOBBE-MEESTER I am greatly indebted for the careful execution and help with the experiments and the analyses in the years 1947 to 1952.

REFERENCES

ARISZ, W. H., Uptake and transport of chlorine by parenchymatic tissue of leaves of Vallisneria spiralis; I. The active uptake of chlorine. Proc. Kon. Ned. Akad. v. Wetensch., Amsterdam 50, 1019–1032, 1947; II. Analysis of the transport of chlorine. Proc. Kon. Ned. Akad. v. Wetensch., Amsterdam 50, 1235–1245, 1947; III. Discussion of the transport and the uptake. Vacuole secretion theory. Proc. Kon. Ned. Akad. v. Wetensch., Amsterdam 51, 25–32, 1948.

ARISZ, W. H., Invloed van remstoffen op het transport bij Drosera tentakels. Verslagen Kon. Ned. Akad. v. Wetensch., 61, 39–42, 1952.

FOUR SPECIES OF EXOBASIDIUM IN PURE CULTURE

BY

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INTRODUCTION

The purpose of this investigation was to study the possibilities of obtaining pure cultures of *Exobasidium.*

The following species of *Exobasidium* were studied:

Exobasidium japonicum Shir., parasitic on Azalea indica.

Exobasidium rhododendri Cram., parasitic on Rhododendron ferrugineum and Rh. hirsutum.

Exobasidium vaccinii (Fuck.) Wor., parasitic on Vaccinium vitis-idaea.

Exobasidium vexans Mass., parasitic on Thea sinensis, causing the blister-blight.

The manner of attack of their hosts is the same for the four species: the affected part of the plant becomes hypertrophic and after some time basidiospores are formed on the exterior of the hypertrophy. When the basidiospores are mature, they are shot from the basidia with some force.

E. japonicum, rhododendri and *vaccinii* form conidia (= sporidia = secondary spores) after the emergence of the germ-tubes from the basidiospores; the conidia are small, fusiform cells, formed in branched chains.

E. vexans differs in its manner of germination from the other species studied. In this species long germ-tubes grow out from the basidiospores, but no conidia are formed.

In the collection of the "Centraalbureau voor Schimmelcultures", Baarn, Netherlands the genus *Exobasidium* was represented by one species viz. *Exobasidium japonicum,* an isolation from Azalea indica, received from Dr. Blumer (Switzerland).

Living cultures of the species dealt with in this paper have been deposited with the collection of the "Centraalbureau voor Schimmelcultures".

SHORT SURVEY OF THE LITERATURE

The genus *Exobasidium* was founded by WORONIN in 1867 (10). WORONIN gave an excellent description of the type species, *E. vaccinii*, and also studied the germination of the basidiospores and the manner of infection of this fungus. He saw that fallen basidiospores could germinate on practically any substratum in a humid atmosphere. Within an hour after placing a slide under a hypertrophy, basidiospores are found on the glass; twenty-four hours later the glass is covered with a white powder of spores. The spores, when shed, often form a septum.

If the air is saturated with water vapour the spores germinate; germ-tubes are formed at both ends of the spore, the contents of the spore move into the germ-tubes and the number of septa in the spore increases to three or four. The germ-tubes continue to grow, occasionally they branch, after some time they begin to form the one-celled, fusiform conidia. The conidia, formed in mass, are loosely connected. The germination on a slide may continue for three to five days, then no further growth is observed.

WORONIN also describes the germination of the basidiospores on the leaf of the host Vaccinium vitis-idaea, which is quite different from the germination observed on a slide. The germ-tubes do not develop conidia, but penetrate into the leaf, either by the stomata or by piercing the cuticle and the epidermis. Within the leaf a mycelium is formed and the affected area of the host reacts by forming a hypertrophy.

BREFELD (1) is the first investigator, who cultivated an *Exobasidium.* He describes and draws a culture of *E. vaccinii* growing in liquid medium. When the tips of the outgrowing germ-tubes had reached the boundary-line between liquid and air, conidia were formed. The development of conidia continued until the medium was exhausted. No basidia were observed. The conidia which Brefeld obtained in his cultures could be used for inoculation of the host.

RICHARDS (8) reports that his attempts to cultivate *Exobasidium* on agar media were not successful.

LAUBERT in "Sorauer's 'Handbuch der Pflanzenkrankheiten'" (5) reports on the genus *Exobasidium* a germination of the spores identical to the germination of *E. vaccinii* as is described by WORONIN.

GADD and LOOS (2) describe the germination of the basidiospores of *E. vexans* in hanging drops. In about five hours germ-tubes grow out from both ends of the spore, sometimes they also develop laterally. Likewise in this species the contents of the spore flow into the germ-tubes, leaving behind an emptied spore-wall.

In another publication the same authors (3) give some more details about the germination of the spores. They observe the development of appressoria on the germ-tubes. These are small, half-spherical organs, which firmly attach the fungus to the leaf. This adherence is of importance for the fine hyphal thread, which, growing out of the appressorium, has to force its way through cuticle and epidermis.

The most favourable conditions for the germination are obtained when the spores are allowed to germinate on a glass slide. This slide is covered by a very thin film of water formed by condensation.

Gadd and Loos in this paper also describe the germination of *E. rhododendri*, which is comparable to that of *E. vaccinii*, as in both species small conidia are produced.

Reitsma and Van Emden (6) also report the germination of basidiospores of *E. vexans*. In a later publication (7) the authors state that they succeeded in cultivating germinated basidiospores on togé-agar during seven days. Germ-tubes of 60 μ length were formed. Unfortunately the culture was lost.

Loos (4) considers *E. vexans* as an obligate parasite, that will never grow on dead organic material, therefore, according to Loos, all experiments to culture this fungus will be doomed to fail.

In a recent paper Wolf and Wolf (9) report their experiments with *E. camelliae* var. *gracilis* Shir., parasitic on Camellia sasanqua. They successfully grew this fungus in pure culture. The isolations were made either by placing fragments of affected leaves on maltagar or by transferring mature basidiospores to agar media. Within a week greyish to brownish, rough, yeastlike colonies had developed.

MATERIAL

E. vaccinii was the first species studied. Material of this fungus growing on Vaccinium vitis-idaea was collected at the Veluwe (Netherlands).

Twigs of Rhododendron ferrugineum and Rh. hirsutum attacked by *E. rhododendri* were received from Switzerland.

Later, several specimen of cultivated Azalea (A. indica) were obtained, which were infected by *E. japonicum.*

Several times tea leaves attacked by blister-blight were received from Ceylon and Indonesia. This material, however, was often in a very poor state and could rarely be used for making isolations of *E. vexans*. Then, some infected tea seedlings were received, which continued to grow in a hot-house, they became the base for the study of living material of *E. vexans* in the Netherlands, as from these seedlings a few young healthy tea plants could be inoculated.

METHODS

The methods generally used for isolating a fungus such as putting small portions of desinfected hypertrophic areas of the plant on agar plates or plating out a spore suspension, or by streaking scratched off particles on agar, did not give any result with these fungi. Either no growth was obtained or saprophytes covered the plate after a few days.

Finally, good results were obtained by starting from germinated basidiospores discharged on a solid surface.

A. *Exobasidium japonicum, rhododendri* and *vaccinii*

Hypertrophic parts of the hosts were kept in sterile Petri dishes; by means of some wet cotton wool a relative humidity of 100 % was secured. After 24 hours a white spot was clearly visible under the hypertrophy. When observed under the microscope this white spot proved to consist of germinated basidiospores, which had already begun to produce conidia. By means of a firm needle with a flattened tip a little of this spore substance was transferred to agar slants. After about 6 days the cultures — which will be described below — began to grow.

A second method, giving the same results, was carried out as follows: Small fragments of a hypertrophy were fixed with vaseline to the inside of the lid of a Petri-dish, filled with agar. By turning the lid somewhat during the first hours of spore discharge, the outgrowing colonies were spread over the agar surface. A disadvantage of this method is that sometimes a plant fragment will fall on the agar thus causing contaminations which outgrow the culture of *Exobasidium.*

B. *Exobasidium vexans*

The first method of isolation described above rarely gave a result. As this fungus does not produce conidia, the germ-tubes were too much damaged when they were scratched from the glass surface. *E. vexans* was therefore always isolated by the second method.

CULTURE MEDIA

Exobasidium vaccinii was cultivated on a series of 25 different solid culture media and on 5 liquid media. The best growth was obtained on the ordinary media such as cherry, potato-dextrose, malt and maltsaleb*agar.

Cultures on maltsalebagar showed characteristic growth forms. The other three *Exobasidium* species also grew well on these media. Attempts to grow the fungus on an agar medium, prepared with a decoction of leaves of Vaccinium vitis-idaea were not very successful, the growth on this medium was very poor.

E. vaccinii cultures were used to study the influence of the temperature on the growth of this fungus. Low temperatures as well as a constant temperature of 28° C. proved to be unfavourable. The normal room temperature (17° — 20° C.) with a slight change between day and night, proved to be the optimal temperature for the growth of *E. vaccinii.* In its cultural requirements, *E. vaccinii* therefore does not differ from the common moulds.

DESCRIPTION OF CULTURES

I. *Exobasidium vaccinii*

Basidiospores discharged in a Petri dish are transferred with a needle to maltsaleb, malt, cherry and potato-dextroseagar in tubes. After 6 days a slight growth becomes visible. The colonies grow concentrically and become somewhat raised, forming half spherical heaps, not unlike bacteria colonies. The colony very soon acquires the shape of a small crater when its border becomes less regular; later, when the culture ages this shape becomes less marked;

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* Saleb is a starch obtained from the corms of orchids growing in the Netherlands.

scattered colonies are growing together, the growth then resembles a coral, showing a yellowish-white, granular and wrinkled surface (fig. 1). Transfers of cultures always show the coral-shaped form of growth only. On malt agar the colour of the aging culture turns dark yellow till brown. Cultures of *E. japonicum* (strain Blumer) show similar growth characters; it therefore seemed very probable that the isolates were indeed those of *E. vaccinii*. Later the identity could be proved by successful inoculations of healthy plants of Vaccinium vitis-idaea with conidia from these cultures (see page 522).

A mount made from a culture shows numerous fusiform cells, the conidia, measuring 15—20 × 2—3 μ. Sometimes also larger mycelial fragments are observed. Always the particles are connected, though very loosely.

The occurrence of the larger fragments appeared to be influenced by the culture medium. On Acer-twig, lupine-stem and tomato-stem mycelial fragments were produced of 30 μ. They also occurred on an agar medium prepared with a decoction of leaves of Vaccinium vitis-idaea.

II. *Exobasidium japonicum*

Young cultures of this fungus exactly resemble those of *E. vaccinii* On further development, however, they show a more regular cerebriform folding of the surface and are never as irregularly wrinkled as those of *E. vaccinii*. The colour on all media is greyish-brown, often the medium covered by the mould discolours; potato-dextrose agar e.g. turns brown.

This fungus also produces conidia about 25 μ long and 2 μ broad.

III. *Exobasidium rhododendri*

At first the cultures are directly comparable to those of *E. vaccinii* but soon the feature of the culture shows a rather flat structure which can best be characterized by comparing it to folded cultures as seen by yeasts.

Mounts of these cultures again show Exobasidium conidia, measuring 10 × 2 μ.

IV. *Exobasidium vexans*

As *E. vexans* was considered to be an obligate parasite (Loos 4) which cannot be grown on dead substances, the cultures obtained from hypertrophic tea leaves were at first very critically watched.

From the fact, however, that identical cultures were obtained from the Ceylon material as well as from Indonesian tea leaves and from the material obtained here in the hot-house through inoculation by the seedlings from Ceylon, it was concluded that the cultures were indeed isolates of *E. vexans*.

Moreover the dull spots on agar media caused by the spore discharge of *E. vexans* were examined microscopically. They always proved to consist of germinated basidiospores. The spores had already

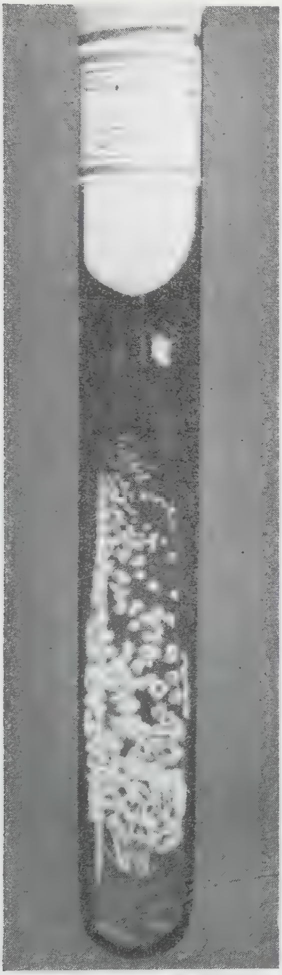

Fig. 1

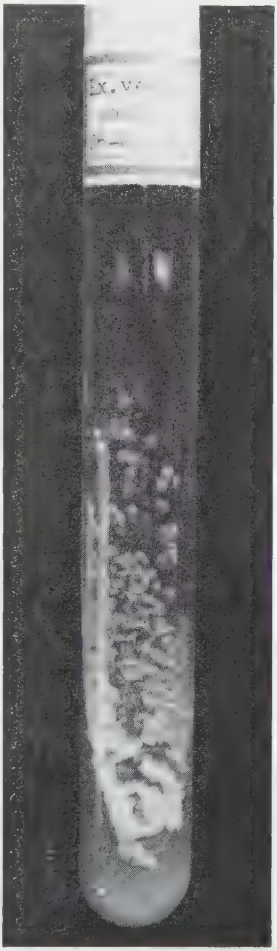

Fig. 2

Fig. 1. Culture of *Exobasidium vaccinii* (Fuck.) Wor. on maltagar.

Fig. 2. Culture of *Exobasidium vexans* Mass. on maltsalep agar.

emptied their contents into the irregularly growing germ-tubes. In later stages also, empty spores could often be found amongst the hyphae. As it is very difficult to cultivate tea plants in a moderate climate, the absolute proof of the identity of the cultures viz. by demonstrating their parasitic power to cause blister blight, could not yet be given. Experiments concerning this point are still in progress.

Young transfers also show the typical feature of scattered half-spherical colonies. By growing together, these separate colonies then form the typical much folded culture (fig. 2).

Conidia are never observed in *E. vexans*. The culture consists of loosely connected mycelium fragments of different lengths. The width of the hyphae is 1—2 μ.

INOCULATION EXPERIMENTS WITH EXOBASIDIUM VACCINII

To obtain a spore suspension the ordinary method of shaking a culture with water proved unsuccessful as the conidia have a strong tendency to clump. Good results were obtained by crushing a culture in mortar; most of the conidia remain uninjured in this process.

A suspension, thus obtained, was sprayed on some healthy plants of Vaccinium vitis-idaea which had been previously well moistened. After 8 days small white spots became visible on many of the young leaves, after 16 days several hypertrophies had developed, identical to those formed under natural conditions.

From these hypertrophies cultures could again be isolated, identical to those which had been used for the inoculation.

Two conditions are of importance for obtaining positive inoculations:

a. The plants to be inoculated should have young sprouting shoots.
b. The culture used for the inoculation should not be older than a few weeks.

SUMMARY

Some methods are described for isolating and culturing *Exobasidium species*. Detailed descriptions are given of cultures of

Exobasidium japonicum Shir.
Exobasidium rhododendri Cram.
Exobasidium vaccinii (Fuck.) Wor.
Exobasidium vexans Mass.

Successful inoculation experiments of *Exobasidium vaccinii* are reported, the fungus being re-isolated from the hypertrophies it had caused on Vaccinium vitis-idaea.

REFERENCES

1. BREFELD, O. (1889), Die Gattung Exobasidium. Unters. aus dem Gesammtgeb. der Mykologie *3*, Heft 8, 12.
2. GADD, C. H. & C. A. LOOS (1948), The basidiospores of Exobasidium vexans. Trans. Brit. myc. Soc. *31*, 229.
3. GADD, C. H. & C. A. LOOS (1950), Further observations on the sporegrowth of Exobasidium vexans. Trans. Brit. myc. Soc. *33*, 19.
4. LOOS, C. A. (1951), The causative fungus. Tea Quart. *22*, 63.
5. LAUBERT, R. (1932), in: P. Sorauer, Handbuch der Pflanzenkrankheiten *3*, 282.
6. REITSMA, J. & J. H. VAN EMDEN (1949), De bladpokkenziekte van de thee I. Bergcultures *12*, 218.
7. REITSMA, J. & J. H. VAN EMDEN (1949), De bladpokkenziekte van de thee II. Bergcultures *18*, 18.
8. RICHARDS, H. M. (1896), Notes on cultures of Exobasidium andromedae and of Exobasidium vaccinii. Bot. Gaz. *21*, 101.
9. WOLF, F. T. & F. A. WOLF (1952), Pathology of Camellia leaves infected by Exobasidium camelliae var. gracilis Shirai. Phytopathology *42*, 147.
10. WORONIN, M. (1867), Exobasidium vaccinii. Ber. über die Verhandl. der Naturf. Gesellsch. zu Freiburg I.B. *4*, 397.

ON THE HABIT, ECOLOGY AND TAXONOMY OF THE BRAMBLES OF THE NETHERLANDS

BY

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Communication no 56 of the Biological Station of Wijster (Dr)

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I. INTRODUCTION

The habit of a plant gives as a rule unmistakable indications as to its ecology, but as it is at the same time a reflection of the hereditary characters on which its taxonomic position rests, it is no wonder that there appear to be quite distinct relations between the latter and the plant's ecological behaviour. This is well exemplied by the brambles.

Among the *Moriferi* or true brambles we meet with several ecotypes; some of these are remarkable for their resistance to low temperatures, some are hygrophilous, xerophilous or sciophilous forms and some show a preference for alkaline soils, and it appears that these five ecological groups correspond with five taxonomical ones, viz. the *Suberecti*, *Silvatici*, *Discolores*, *Glandulosi* and *Caesii*, groups that have been founded by the taxonomists in the usual way on morphological, genetical and geographical grounds, and not on ecological ones.

Because of this close parallelism between habit, ecology and taxonomic position it seems desirable that the study of the very numerous taxonomic units of which this difficult genus is composed, should not be confined to their morphological characters, geographical range and origin, but that it should also consider their structure and mode of life.

The principal aim of this paper is to discuss a number of morphological and ecological characters that may be of importance for distinguishing the various species and infraspecific taxa, and which throw some light on their occurrence in a definite environment. It is not my intention to give a complete list of these characters, for a study of a restricted number will suffice to illustrate my meaning. In the concluding chapter the various attempts to arrive at a classification of the *Rubi* will be surveyed; special attention will be paid in this survey to those taxonomic units that occur in the Netherlands, viz. to a part of the *Moriferi* or true brambles, the raspberry and the stone raspberry (*Rubus saxatilis* L).

II. STRUCTURE

It has since long been recognized that a plant's habit (its phenotype) is determined by the action of the environment on its hereditary structure (the genotype). The structural characters of the brambles, their vigour and term of life, their fertility etc. depend on differences in the supply of nutrients and in that of water, light and heat. The deviation from the average type, however, is but seldom so profound that it becomes difficult or impossible to recognize the taxonomic unit to which a particular specimen belongs. Nevertheless, as it is not excluded that the variability of the phenotype may cause difficulties, it is of importance to gain some insight in the way in which the various parts are influenced by the environment.

A study of the growth forms exhibited by our native brambles leads to the conclusion that there are two main types, viz. plants with several erect or suberect stems and plants provided with arcuate stems and branches and, as the stems spring from the same base, more or less dome-shaped in contour (cf. fig. 1). In plants belonging to the first-named type the shoots develop from adventitious buds formed by the roots, and they grow on the whole more or less straight upwards, although it is not excluded that their upper parts may in the end bend down under the increasing weight of the foliage. In plants belonging to the second type the shoots very soon begin to deviate from the vertical position and assume an arcuate form, and as the various shoots bend down in different directions, the contour of the plant becomes more or less dome-shaped. In late summer or autumn the shoots have curved down so far that their tips come into contact with the soil, and this is a phenomenon that is observed but very rarely in the plants belonging to the other group. Under extreme circumstances, e. g. when the plants grow in a moist

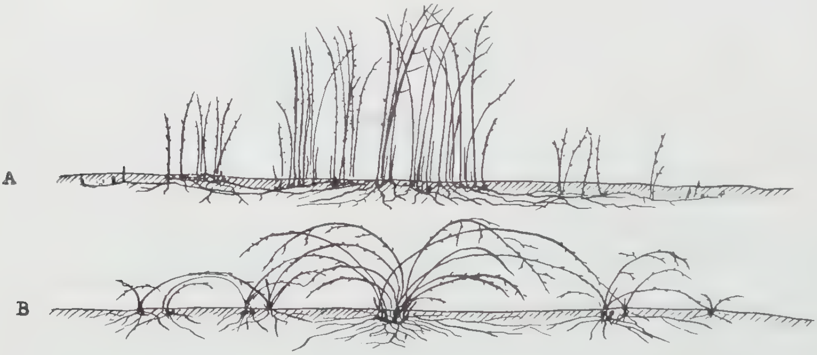

Fig. 1. The two growth forms of our native brambles. A. suberect type, shoots developing from buds on the roots ; B. dome-shaped type, with rooting stemtips

humus, rich in nitrogen, the stems of the plants belonging to the second type may become prostrate. On the other hand, when they grow in dense brushwood, the stems may straggle over the latter and reach a height of 4 or 5 meter, occasionally even of 10 meter.

A rich supply of nitrogen, and deep shade in combination with a high degree of humidity may change the plant's habit so profoundly that it becomes difficult, even to a trained botanist, to determine its taxonomic position, for in that case the change may not be confined to the size of the plant as a whole, but it may also affect the differentiation of the various parts and their relative size and position (leaf shape, indumentum, presence of glands, flower colour etc.)

Noteworthy is the short term of life of the shoot or turion. It flowers as a rule but once, usually in the second year, and dies when the fruits are ripe. The shoots of *R. tomentosus* Borkh., a species of South-central Europe, may flower already in the first year. Very vigorous turions, on the other hand, may live a year longer, flowering for the second time in the third year, but this is always exceptional. In accordance with this short term of life, the bark is but weakly developed and lenticels are absent; an exception forms *R. caesius* L, the dewberry.

The surface of the turions is usually beset with outgrowths in the form of prickles, which may break off above the base leaving a pustule, further bristles and other kinds of hair and stalked or sessile glands, and it may be covered with a layer of wax. In the development of the prickles the subepidermal tissue may take part or they may be entirely of epidermal origin, e. g. in *R. caesius* L.

The prickles may be inserted with regular intervals in the ribs of the shoots (e. g. in some of the *Silvatici*) or they may be spread irregularly over the whole shoot, in which case they may be collected in more or less distinct groups, and they may be all of the same size (in the homalacanthous forms) or of different size (in the heteracanthous forms). In the latter group they may gradually pass into eglandular or glandular bristles or into softer hairs. Their shape too varies considerably. Sometimes they show a strongly enlarged base and they vary between laterally flattened and subterete. Short, broad and rather blunt prickles are alternating with slender, long and sharply pointed to nearly needle shaped ones (*R. fissus* Lindley). Finally they may be straight and either patent or subpatent, or they may be curved or uncinate. The indumentum too shows considerable differences. It may be dense and regular, but also more or less sparse and the hair may be long or short and they may occur singly or in fascicles. The short stellate hairs may spring from a single epidermal cell or, more rarely, from a group of such cells. This complicated system of trichomes and emergences constitutes one of the most valuable means for distinguishing the species of the *Moriferi* or true brambles (fig. 2). The branching of the annual shoots may vary considerably. In the *Suberecti* it is sometimes entirely absent although there are also species with strongly branching shoots in that group.

Moreover, in shoots that normally remain unbranched, branching

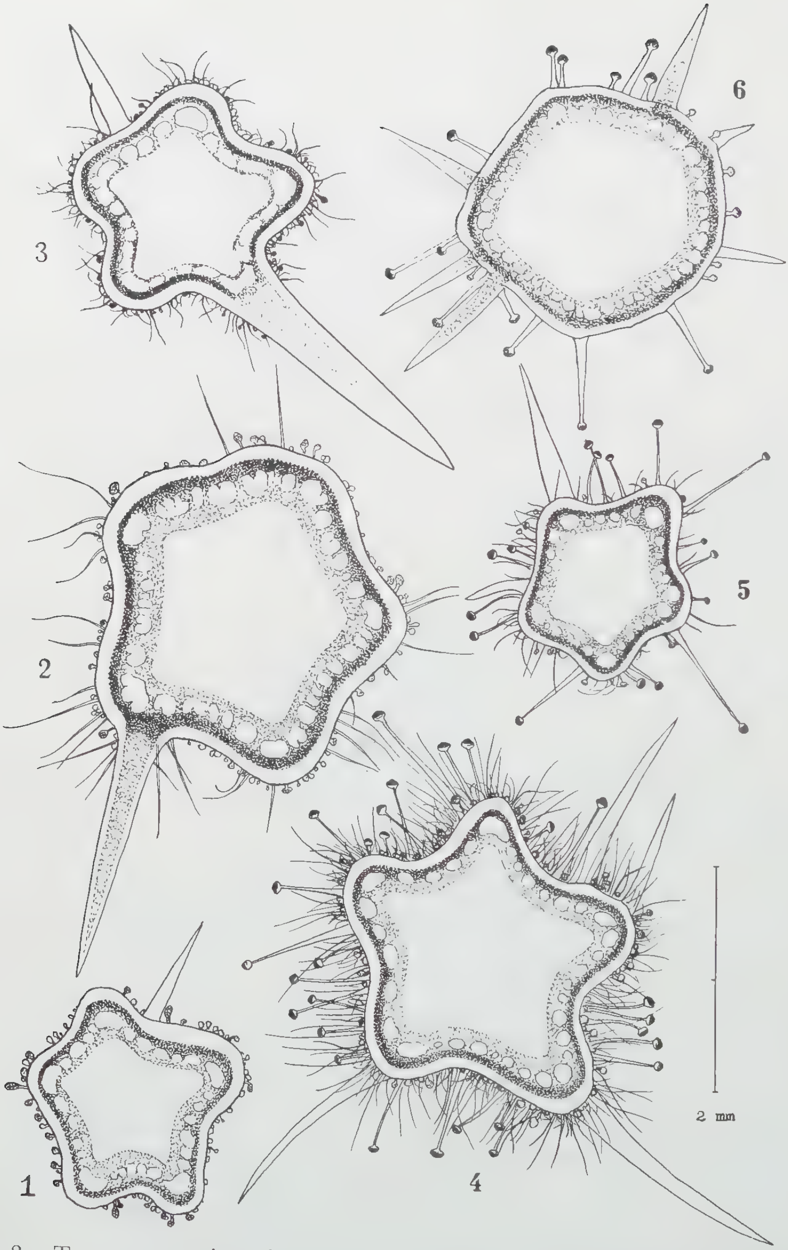

Fig. 2. Transverse sections through turion-tops of: 1. R. fissus Lindl. (Suberect.); 2. R. silvaticus Wh. et N. (Silvatici); 3. R. ulmifolius Schott. (Discolores); 4. R. mucronifer Sudre (Appendiculati); 5. R. Bellardii Wh. (Appendiculati) and 6. R. caesius L. (Caesii)

may be induced by a mechanical injury of the growing point. In vigorous shoots the leaves bear generally two serial buds in their axil; the upper bud develops first and should therefore be considered the main bud. When the shoot that develops from this bud is damaged or its growth inhibited, the second bud provides a substitute. The lateral branches of the 1st order may, in strong plants, produce lateral branches of the 2nd order. According to Focke accessory buds would be rare in the less vigorous species e. g. in some *Glandulosi*. In that case damaged shoots are replaced by new ones arising from buds at their base.

In *R. caesius* L too, several side shoots are said to develop from the base of the main shoot although branching is a common feature here. On exceptionally strong shoots a second axillary bud may be plainly visible. However, this bud will only rarely develop into a branch.

The differences in shape (habit) discussed above, how striking they may be, are of little value for distinguishing the species. Even the erect growth form, so often met with in the *Suberecti*, is not found under all circumstances. When *R. nessensis* W. Hall is growing in a dark and humid wood, with a layer of humus rich in nitrogen, its shoots may be nearly prostrate. The taxonomical differences, therefore, must be looked for elsewhere.

The way in which trichomes and emergences are distributed on the turion and the character of these appendages are to be considered distinguishing marks of much greater importance and it is on these characters that the subdivision of the *Moriferi* is chiefly based (*Suberecti*, *Silvatici*, *Discolores*, *Appendiculati*). The presence of a layer of wax on the turion of some species is also a fairly constant feature, though it is found in several *caesius* hybrids too.

The foliage leaves of our brambles show their most typical form near the middle of the 1st year shoots or turions. They are composed of 3—7 leaflets and palmate or pedate. In the latter case the outward pair of leaflets spring from the stalks of the inward pair (Fig. 3).

According to Focke 4 types of compound leaves are to be distinguished with the *Moriferi*, viz:

1. the trifoliate leaf;
2. the pedate quinquefoliate leaf, derived from the trifoliate leaf by the division of each of the outward leaflets into 2 separate ones, the leaflets' stalks, however, remaining united with that of the odd leaflet;
3. the palmate quinquefoliate leaf, derived from the former, by the splitting of the side leaflets' stalks to the base, the 5 stalks originating from one centre;
4. the septemtrionate leaf, which may be looked upon as having originated from the quinquefoliate, palmate leaf by a symmetrical division of the odd leaflet into 3 separate ones; it may therefore be regarded as a quinquefoliate leaf with a trifoliate odd leaflet.

A simple quinquefoliate pinnate leaf occurs as an exception with the dewberry (*R. caesius* L.) Pinnate leaves, however, do occur frequently with the Idaeobati, the group to which our wild raspberry belongs.

According to Focke (1877, p. 12) trifoliate leaves would be present in all species, and it would be the normal form of leaf in many weak growing brambles. In a small number of species it is even the only form of foliage leaf.

The odd leaflet of the brambles is always provided with a long

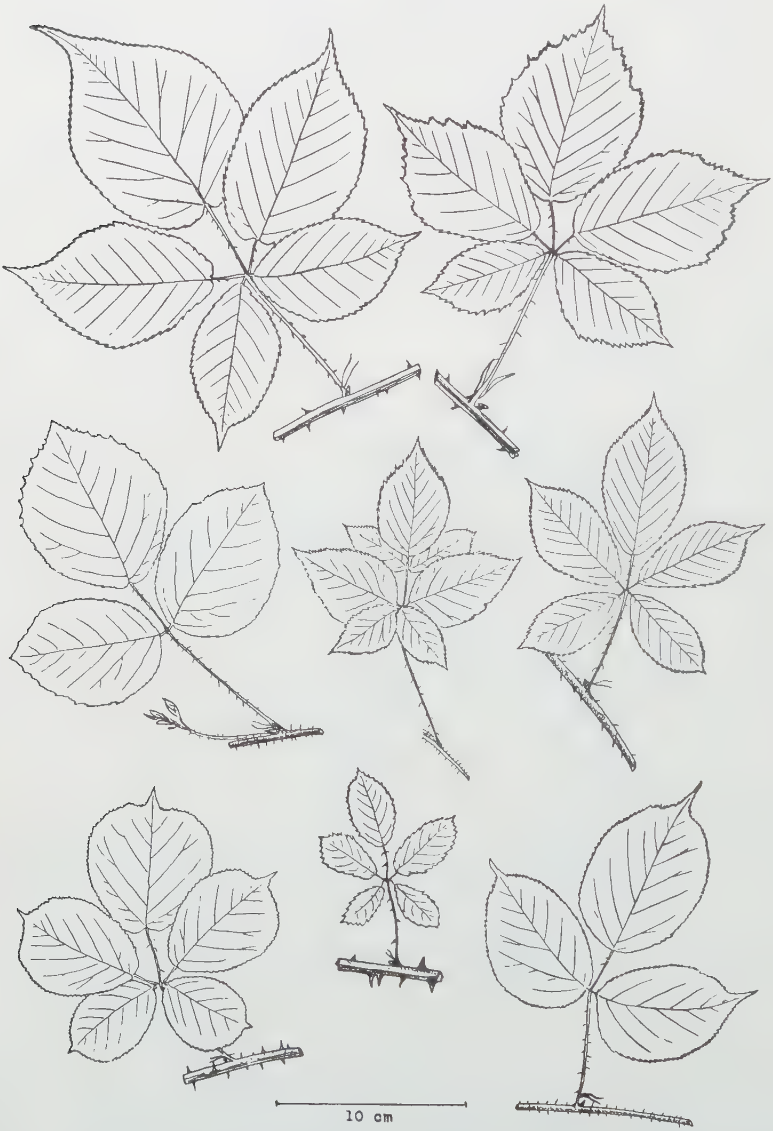

Fig. 3. Leaf shape of dutch brambles, At the top, on the left R. nessensis W. Hall, on the right R. gratus Focke. In the centre, from left to right R. egregius Focke, R. fissus Lindl., R. Arrhenii Lange. Below, from left to right R. mucronifer Sudre, R. ulmifolius Schott, R. Bellardii Wh.

stalk, the inner pair of leaflets possess distinctly shorter ones and the outer pair are short stalked or subsessile.

At the base of the petiole stipules are present and the latter are of various width and implanted at various heights of the petiole.

The petioles themselves show sometimes on their upper side a groove extending from the base to the top or over part of their length; when it is missing the petioles are either flat or slightly raised.

Between the length of the petiole, that of the petiolules and that of the leaflets there is a fairly constant proportion, provided that well developed leaves, like those that are present near the middle of the turion, are compared. The general appearance of the leaves is for an important part determined by them; e.g. comparatively short-stalked and wide leaflets will overlap, whereas long-stalked and narrow ones do not overlap. The lateral leaflets are always more or less asymmetrical, like the leaves of the elm.

When describing the leaves special attention is to be paid to the odd leaflet, but as has already been pointed out, the description should be based on a leaf from the middle of a turion. The number of lateral nerves is no reliable feature.

In young leaves the surface along the lateral nerves is plicated and these creases may remain visible with some species in the adult state, e.g. in *R. plicatus* Wh. et N., especially when the leaves develop in full light; in the shade the creases may almost completely disappear.

The structure of the leaf margin, although always dentate, varies with the species; the teeth may be large or small, of the same or of different size, and simple or compound. The shape of the teeth (wide or narrow, sharp or blunt) is best judged near the middle of the blade. Colour and glossiness of the leaves depend partly upon environmental factors, but they may nevertheless be regarded as characteristic for some species; those of *R. Arrhenii* Lange and *R. nessensis* W. Hall e.g., as a rule being distinctly nitidous. With regard to the shape of the odd leaflet, it seems best to follow FOCKE's classification:

1. Greatest width in the middle.
    - *a.* the margin of the leaflet is regularly curved towards top and base: narrowly and broadly elliptical leaflets;
    - *b.* the margin runs straight from the middle towards top and base: rhomboidal leaflets;
    - *c.* the margin is curved in the part above or below the middle and straight in the other part;
    - *d.* the margin is more strongly curved in the upper half than in the lower one;
2. Greatest width below the middle, with the same subdivision as mentioned above.
3. Greatest width above the middle.

The base of the leaflet may be rounded, cuneate, truncate or narrowly to broadly cordate. The top of the leaflet too is often very characteristic; it may be acute, subacuminate, acuminate or gradually to suddenly contracted.

The flowering shoots vary according to their position near the base or the top of the biennial turion. With weak-growing species the flowering twigs often spring from the subterraneous axes and in this case their shape is intermediate between that of a turion in its first year and that of the ordinary flowering shoots, and they bear an extremely complicated inflorescence of which the branches are often subtended by leaves, so that they sometimes resemble a series of separate inflorescences. The lower flowering shoots springing from the turion resemble the flowering shoots springing from the rhizome and this resemblance is the more striking, the later they come into flower. Therefore, when comparing flowering shoots, one should take shoots arising from the middle part of the turio. Towards the top the inflorescences are often reduced.

The inflorescence of the brambles comprises a terminal flower, which is also the earliest one. Although racemes (lateral axes one-flowered) and compound racemes (lateral axes compound) are strictly speaking inflorescences that lack a terminal flower, it is customary to apply these terms to the inflorescences of the brambles. The racemes may be everywhere of the same width or they may become narrower towards the top. The lateral branches may sometimes form regular dichasia. Parallel to the formation of accessory buds on the annual shoots, accessory branchlets fairly often develop on the axis of the inflorescences; they are formed between the main branchlet and the bract. The bracts themselves are either simple or divided into 2 or 3 slips, and transitions from bracts to foliage leaves are not rare.

The terminal flower opens first and it is followed by the terminal flower of the lowest lateral branchlet; subsequently the terminal flowers of the remaining branchlets begin to open. The lateral flowers of the lower branchlets therefore open, as a rule, simultaneously with the terminal ones of the higher branchlets.

Below the terminal inflorescence some axillary flowering shoots may be present. The higher ones start flowering before the lower ones. With some species a second inflorescence usually develops below the old inflorescence, which bends downwards under the weight of the fruits.

As to the petals and sepals, it should be remarked that shape and colour of the petals, the angle of inclination of the sepals and the presence of appendages on the latter may be of importance for the identification of the species (Fig. 4).

The sepals may change their angle of inclination after flowering or during the ripening of the fruit; they may be reflexed, erect or patent. They may wither while the fruits are ripening or they may remain green and juicy. The shape of the petals is fairly constant for each species although deviations do occur.

The relative length of the stamens, in comparison with the styles, and their position with regard to the latter are specific characters.

According to Focke a moist and rich soil would, in some species, produce longer stamens than a dry and poor one would do. The angle of inclination of the stamens during and after anthesis is also of importance. Short stamens will show less change in direction than long ones. After flowering the stamens may soon whither and in that case they will be leaning against the fruit or they may keep up a certain distance.

The pollen of some species is composed of regular, well-shaped grains, e.g. in *R. ulmifolius* Schott, *R. caesius* L and *R. tomentosus* Borkh. As a rule part of the grains is deformed.

The anthers may be hairy or smooth; the filaments are white, greenish, pink or red and the same applies to the styles. Otherwise there is little variation in these organs. The colour of the floral parts is fairly constant in some species, variable in others (*R. vestitus* Wh. et N.). Some species possess faintly-scented or completely scentless flowers.

When the fruits of the true brambles (*Moriferi*) are ripe, they are, together with a part of the receptacle, released from the stalk. The fruits of *R. caesius* L are the only ones that may be picked, like those

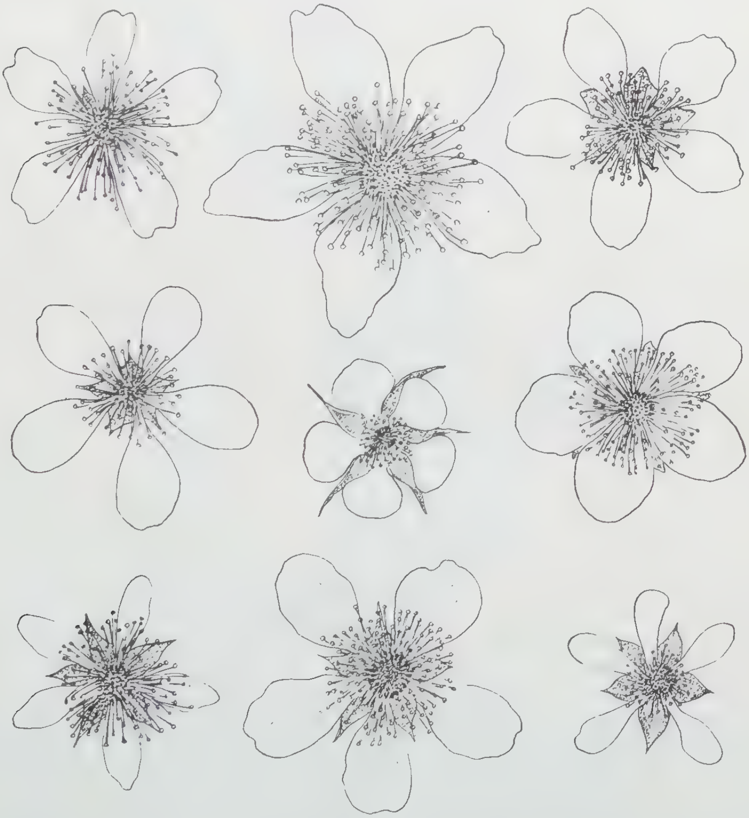

Fig. 4. Flower shapes of dutch brambles. Top, from left to right R. carpinifolius Wh., R. gratus Focke, R. ammobius Focke. Centre, from left to right R. mucronifer Sudre, R. Arrhenii Lange, R. chlorophyllus Gremli. Below, from left to right R. rudis Wh., R. badius Focke and R. serpens Wh.

of the raspberry (subgenus: *Idaeobatus*), while the whole receptacle is left behind.

Size and shape of the drupes vary on the whole insufficiently to serve as distinguishing characters. In some species, e.g. in *R. ulmifolius* Schott and in *R. tomentosus* Borkh. they differ indeed in shape and colour, but these species are already easily recognisable by the presence of several other differentiated characters.

III. Ecology

To recognize the brambles in the field, some insight into their mode of life, development and growthform is desirable. The european *Moriferi* belong to the "suffrutices" or "half-shrubs" of Warming, or to the "Holzstauden" of Drude. For the more or less exceptional case of the *Rubi* the latter author proposes the term "Schösslingsträucher". This means that they are provided with a woody persistent stem base, below or just above the soil surface and that every year

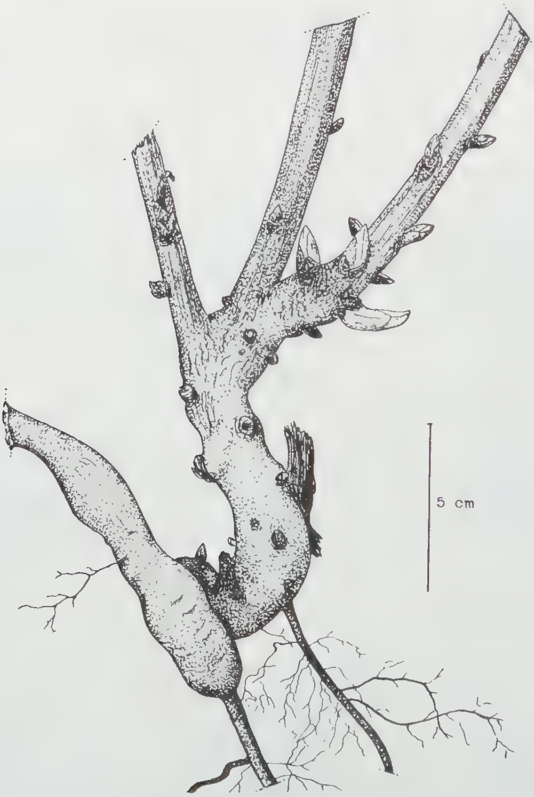

Fig. 5. Stembase of an old plant of R. gratus Focke. At the base of the youngest turion some large buds and several smaller ones are present; the latter as a rule remain dormant. Drawn in the middle of February

new shoots are produced by this part (Fig. 5). These shoots become woody in their turn. As a rule they are hapaxanthic (flowering once only).

The ripe fruits are often spread by birds and other animals.

The germination of the bramble seeds is irregular. When the seeds are sown immediately after they have been removed from the fresh fruits, they may germinate before the winter sets in, but as a rule they germinate next spring. It also happens that germination is postponed for another year (Focke 1877).

The cotyledons of the seedlings are ciliate and by this character they are in the field easily distinguishable from similar seedlings (Fig. 6). The first foliage leaves are simple and but superficially

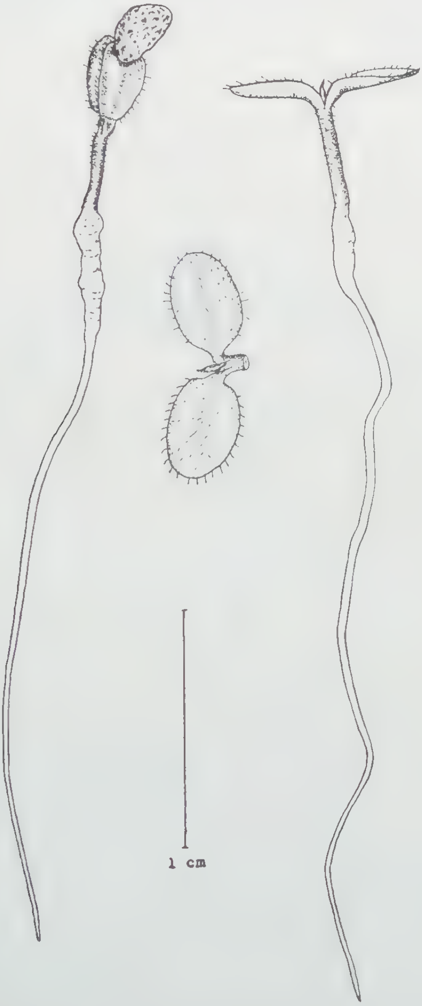

Fig. 6. Seedlings of R. egregius Focke, March 18th, 1950

incised, but the next ones, though still undivided, are lobed or cleft.

Whether the seeds germinate quickly or more slowly, probably depends on their power to absorb moisture and this in its turn depends on the weakening of the thick seedcoat, which differs individually, but the germination is also strongly influenced by the environment.

Still there appear to be differences between the various taxonomic groups: seeds of *Glandulosi* and *Corylifolii* germinate, according to FOCKE, as a rule during the first spring, while the seeds of the taller *Suberecti* and *Silvatici* generally remain dormant until the next year.

The brambles spread not only by means of seed, but also by a strong vegetative propagation, namely by means of the tips of the stem, that in autumn come in contact with the soil and strike root, or by adventitious shoots sprouting from the roots at some distance from the parent plant (Fig. 7). Many species root easily from the stem tips (Fig. 8), e.g. *R. gratus* Focke, *R. pyramidalis* Kaltenb., *R. vestitus* Wh. & N., *R. badius* Focke, *R. flexuosus* M. & Lef. and the *Corylifolii*.

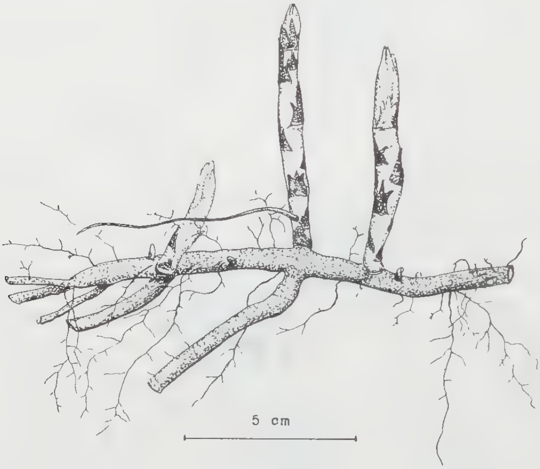

Fig. 7. Root of R. nessensis W. Hall with buds and young shoots. Drawn on February 15th, 1951

The *Suberecti*, on the contrary, do not or only rarely develop roots from their turions, but they form adventitious shoots in profusion.

Besides the three methods of propagation mentioned above, viz. by normally fertilized seeds, rooting stem tips and adventitious buds on the roots, a 4th method of propagation exists in our native brambles, viz. by pseudogamic seed formation. This is a form of apomixis or multiplication without fertilization found in plants, that originally possessed a normal sexual propagation. In this case the seeds develop agamospermously, which means without the fusion of male and female sexual cells (see survey mentioned below)

Survey of the apomictic phenomena in the Angiospermae (After GUSTAFSSON, 1946).

APOMIXIS

Agamospermy Reproduction by means of seeds (disseminules)			Vegetative reproduction Reproduction by means of bulbs, bulbils, runners, layers, etc. (propagules)
1.	2.	3.	
Sporophyte	Sporophyte	Sporophyte	1. Sex-organs and gametes normal. Sterility phenotypically determined. Propagules arising outside the flowering region.
EMC's	Somatic cells		
(Diplospory)	(Apospory)		
Gametophyte	Gametophyte	(Adventitious embryony)	2. Sex-organs normal or deformed. True sterility phenomena. Propagules arising outside the flowering region
Egg-cells	Vegetative cells		3. Sex-organs normal, transformed or deformed. True sterility phenomena. Propagules arising instead of or besides flowers; frequently germinating when still on the plant (vivipary).
(Parthenogenesis)	(Apogamy)		
Sporophyte etc.	Sporophyte etc.	Sporophyte etc.	

If induced by pollen: pseudogamy (Focke, 1881)

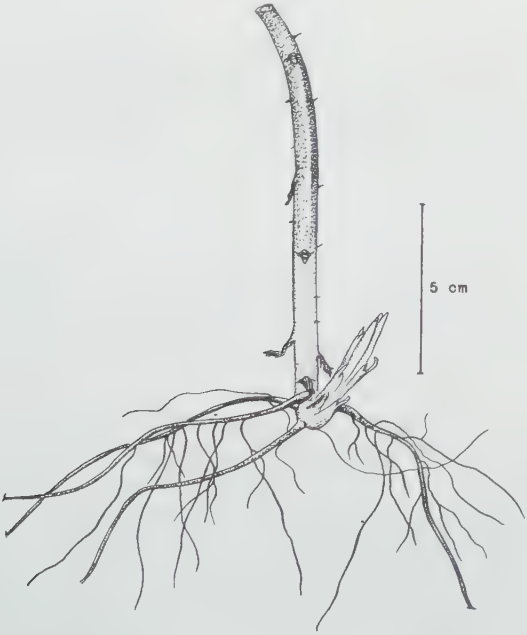

Fig. 8. Rooting stem-tip of R. gratus Focke. Drawn in the middle of February

By pseudogamy is meant the formation of seeds after pollination but without fertilization, the pollen acting as a stimulus. Gametophytes are formed here either from vegetative cells of the sporophyte by mitotic division (apospory) or from embryo-sac mother cells, the gametophytes possessing an unreduced chromosome number (diplospory).

This asexual way of seed formation predominates with the bulk of the European *Rubus* forms, although always some embryos (1–10 %) seem to be developing from normally fertilized egg cells.

Vegetative multiplication occurs in all brambles and is the most common method of propagation in many hybrids (e.g. *R. caesius* × *R. idaeus*) as well as in plants with sterile flowers. By this means sterile or but slightly fertile brambles may locally form large clones.

The dropping of the leaves varies for the different species, but can also be hastened or delayed by various circumstances.

In general brambles growing in the shade of trees, particularly in pine plantations keep their leaves a long time, often until the next growing season. *R. Sprengelii*, *R. badius*, *R. gratus* and *R. flexuosus* are under these circumstances often semi-evergreen or evergreen. In the open *R. ulmifolius* and *R. badius* often keep their leaves far into the winter. The first brambles to loose their leaves are the *Corylifolii*, *R. caesius* included, and the *Suberecti*; the latter are often already leafless before frost sets in. When they are frozen, many more bramble leaves are dying off, one of the reasons being frost damage to the connecting tissues between turion and petiole and between this and the stalks of the separate leaflets. These connecting tissues appear to undergo a swelling and show a ravelled mass after thawing, the leaf stalks sometimes loosely swinging from the vessels before dropping altogether. Brambles that are stretched out flat on the wood floor, often keep their foliage until the young leaves become visible.

By exception leaves of the "last year" may be met with on the plants during summer, among the newly developed foliage. During very cold and dry periods, however, nearly all species will drop their leaves. The sprouting of the leaves shows here slight differences with the various species occurring in a particular locality. The flowering time, on the other hand, is highly specific. The earliest flowering brambles are the true *Suberecti* (*R. nessensis*, *R. fissus*, *R. plicatus*, *R. sulcatus*), the first-named species at the same time having the shortest flowering period.

R. caesius L. and the *Corylifolii* too are early flowering, just like *R. carpinifolius*, *R. Bellardii* and *R. hirtus*. The two first mentioned species, however, are flowering a second time in September and October, and this applies also to *R. badius*, *R. vestitus* and *R. flexuosus*.

In the previous chapter some remarks have already been made on the anthesis. As a rule the flowers are homogamous, which means in this case that the stigmata are receptive when the anthers of the outer stamens are opening. Because of the spreading position of the stamens self-pollination is difficult, but many insects are visiting the flowers. The number of *Hymenoptera*, *Diptera*, *Coleoptera* and *Lepidoptera* that have been observed on bramble flowers (cf. KNUTH 1898, T. II, prt 1, pp. 355—357) is extremely large (round 100 species).

Within the circle of stamens the nectarium lies like a ringshaped wall round the group of ovaries, so that insects with a short proboscis too may reach the hidden nectar and cause pollination. Honeybees (*Apis mellifica* L) and species of *Halictus* are regular visitors, and this applies also to the raspberry beetle (*Byturus tomentosus* F.). This busy visiting of insects gives ample opportunity for cross- and self-pollination and for pseudogamy.

The production of fruits is extremely variable. Slight fertility in spite of rich flowering rouses the supposition that we are dealing with a hybrid, but locality factors too seem to have a great influence. According to FOCKE *R. caesius* would be a free producer of fruits on chalky sand dunes, while it would be a poor bearer elsewhere. *R. nessensis* often produces but few fruits, but is, like other *Suberecti*, often flowering twice in the same season.

As to the condition of the soil, we may state that most brambles prefer a moist medium of mixed composition, rich in organic substances. It should not be too poor. Where sand is mixed with loam or marl brambles will soon appear. On rather poor and acid sandy soils in heath-districts may be found: *R. fissus*, *R. plicatus*, *R. affinis* and *R. gratus*, provided that there is a sufficient supply of moisture. Our brambles are restricted to districts where long periods of drought are lacking. In S. and Eastern Europe they are already distinctly scarcer than in the middle of the continent. Localities that are too moist, seem to be avoided. Bog-preferring brambles are not found among the European *Moriferi*.

Prickles, bristles, glandular and eglandular hairs on the surface of the turions may serve as a means of defence against herbivorous animals, and the prickles may at the same time serve as climbing organs enabling the turions to reach a considerable height in the midst of the surrounding scrub. The prickles are then functioning as a means to prevent the sliding back of the turion.

The need of light is not the same for the various groups and species. The *Glandulosi* are, as a rule, typical forest plants, thriving well in shade or tempered light. On the other hand species like *R. plicatus*, *R. ammobius*, *R. nitidus* and *R. ulmifolius* do not seem to be at home in woods, where they change their aspect a great deal and often fail to produce flowers. *R. egregius* and *R. silvaticus* again are species, that generally remain restricted to woods, at least in our country. It is difficult to say anything definite in this respect, because atlantic species adapted to a moist climate, may seek refuge in forests when they are growing in more continental parts, whereas in the atlantic zone they prefer the open field. This behaviour may often be due to their frost resistance (see below). Moreover many specific and individual differences exist.

The research work of the Finnish botanist PERTTULA (1941) has shown that the capacity of a species to produce seeds and to spread is highly influenced by the plant community of which it forms part.

His conclusion is that each vegetation unit possesses a specific degree of fertility, i.e. of fruit and seed formation, as well as a specific germinating power in their seeds. These units are characterized by qualitatively and quantitatively differing seedlings and by a special ability to vegetative reproduction. PERTTULA shows that vegetative reproduction is a very common phenomenon. More than 80 % of the plant species examined, whether growing in woods, meadows or on rocks, are provided with means for vegetative reproduction, 60 % of these being, in addition, able to migrate easily. He enumerates several vegetative means of spreading, but he does not mention seed formation by agamospermy.

GUSTAFSSON (1943, p. 192) says in this respect: "in the degree that a species increases its power of vegetative propagation and migration, in that degree will its capacity for sexual reproduction be extinguished" and he continues: "is it too bold to draw from this the conclusion that the system of hormonic balance that has evolved in the course of ages in respect of the generative apparatus should gradually be put out of function by the ever-increasing vegetative multiplication? May not agamospermy in the same way imply that the vegetative hormons develop at the expense of the generative ones?"

If the existence of this correlation could be proved, much would become clear that at this moment remains difficult to understand in the behaviour of the various Rubus forms under differing ecological circumstances.

Lastly, as to the climatic influence, remarkably large differences exist among the species with regard to frost resistance. Frost resistance often seems to be important in determining the geographical distribution. Especially bare frost, i.e. frost without a cover of snow, is fatal to many species. The bramble floras of England and France seem to contain many more frost-susceptible forms than e.g. that of northern Germany; this is to be understood in connection with the more frequent occurrence of dry, bare frost in the latter region. In the mountains of Central Europe the number of *Glandulosi* and *Discolores* quickly increases. In Scandinavia and elsewhere in Northern Europe the *Suberecti* become more frequent, increasing in number both of individuals and species, while they disappear in the South. Many *Silvatici* seem to prefer an Atlantic climate.

IV. TAXONOMY

The cytological, genetical and ecological study of the true brambles (*Moriferi*) during the last decennia has revealed a great deal on the character of the *Rubus* "species" and their origin. An interesting survey has been given by the Swedish cytologist ÅKE GUSTAFSSON in his book: "The genesis of the european blackberry flora" (Lund, 1943).

The greatest part of the numerous forms of the European *Moriferi* appeared to be polyploid (mostly tetraploid), which would imply a hybrid-origin. A fair number of species had already been grown from seed by W. O. FOCKE before 1877, and they all proved to be "true to type", which means that, in spite of prevalent cross fertilization, the seedlings always show a close resemblance to the motherplant. Moreover brambles are, as we have already discussed, easily propagated vegetatively and they are able to enlarge their area quickly in this way.

This coming true from seed has contributed to the opinion that one is dealing here with true species. Still, in nature several *Rubus* species may be growing in each other's company and the frequent insect visits cause a liberal amount of cross pollination.

As previously explained, cross fertilization between the various forms is not at all common. Part of the polyploid pollen is generally sterile, and the pollen tube is apparently not always able to reach the embryosack. The production of fruits and seeds in these cases is due to the development of diploid gametophytes or of adventitious embryos. These apomictic seeds germinate normally and reproduce as a rule the exact image of the parent plant.

It is clear that this agamospermy explains the "coming true from seed" of a *Rubus* species. However, not all species are showing agamospermy. A relatively small number of species appeared to be diploid. For Europe these are, as far as now known, *R. ulmifolius* Schott, *R. tomentosus* Borkh., *R. incanescens* Bert. and *R. mosschus* Juz., and perhaps also *R. Bollei* F., from the Canarian Islands.

These diploid species possess well-developed, fertile pollen and this may be used for the fertilization of other forms. At the same time they appear to be self-sterile. First-generation hybrids too may produce fertile pollen. These facts are based chiefly on painstaking investigations carried out by LIDFORSS (1905—07 and 1914), CRANE and DARLINGTON (1927), CRANE and THOMAS (1939, '40), DARROW (1931), DARROW and WALDO (1933) and ROSANOVA (1934, 1938); FOCKE (1877) was the first to start hybridization experiments.

The earlier objection, according to which many Rubus "species" comprised in the Linnean species *R. fruticosus* L would be no more than varieties, forms and hybrids, has therefore lost much of its strength. However, it is true that too diligent Rubus describers ("name-hunting batologists") during the last 150 years have gone too far in the splitting up of the old species. The index of SUDRE's monograph "Rubi Europae" (1913) comprises according to GUSTAFSSON, 1943, ± 3350 latin names. Many of these names apply to primary hybrids or to very local varieties. A large part, moreover are synonyms.

The morphological way of distinguishing species and forms does not always lead to satisfactory results. Difficulties, for instance, are met with, when we try to identify European *Corylifolii* (*R. caesius*-hybrids). Some authors distinguish a large number of forms in this group (FOCKE, E. C. GUSTAFSSON) while others, like SUDRE, apparently shrink back for an extensive splitting of these *Caesii* Focke (= *Triviales* P. J. Müll.).

In connection herewith Å. GUSTAFSSON (1943; p. 25—26) makes the following remark: "By the morphological method of determination we settle nothing but an external and frequently rather vague similarity to a certain Moriferi veri-type. This summary treatment in SUDRE's monograph is one of its weak points, since many Corylifolii are well worthy of a careful study."

"SUDRE's method of classifying the *Moriferi veri* emanates from the fact already shown by FOCKE in 1877 and 1903 that about 75 to 100 blackberry types are spread over large areas and at the same time are so distinct that after a few years' study a taxonomist can distinguish them from one another. Around these, what I call, circle-species he grouped the great mass of named blackberries, several of which are similarly widely distributed and rather distinct, others comprise swarms of more or less unimportant forms, and, thirdly, some merge into neighbouring circle-species. Hybrids — secondary as well as primary — are placed by SUDRE under the circle-species (or microspecies) which they resemble most closely. Descendants from for example the cross of *R. tomentosus* and *R. ulmifolius* are classified either as *R. tomentosus* × *ulmifolius* (= *R. tomentellifolius* Sud.) or as *R. ulmifolius* × *tomentosus* (= *R. pulverulentus* Sud.). These reciprocal markings signify of course great gratuitousness and are condemnable from a genetical point of view." And a little further on: "Most of the 1930 brambles listed in "Rubi Europae" display a localized distribution, though about one hundred types are, as mentioned above, spread over great parts of the European continent. This astounding confusion of local and widely distributed types is caused simply by the occurrence of pseudogamy (i.e. autonomous embryo-formation accompanied by sexual endosperm development), maintaining in nature heterozygous segregates and hybrid derivations. Most of the widely distributed types consist of small, rather uniform populations which continually produce some rare aberrants by means of hybridization or segregation. Primary hybrids breed sexually. Sooner or later pseudo-gamous types appear in their progenies, combining genes and chromosomes in a new manner. The local floras are built up of some wide-spread types, crosses between these, and segregated apomict swarms more or less selected to the local environments. Now and then some segregates enjoy an increased vitality and a potent capacity of seed propagation — in addition to the multiplication by rooting stemtips — and will spread widely."

When this point of view is generally accepted, we may expect the development of a classification based on genetics. However, in the near future the present, morphological classification will have to serve as a starting-point for the new one. So long as genetical research has not made such progress that a classification can be built upon it, we will be obliged to stick to the morphological system.

To give an impression of the systems built up by W. O. FOCKE (1903—1914) and H. SUDRE (1913), their classifications are reproduced below.

In FOCKE's "Species Ruborum" (1914) the genus *Rubus* is subdivided into 12 subgenera in the following way:

I. *Chamaemorus* F. (1 species)
II. *Dalibarda* F. (5 species)
III. *Chamaebatus* F. (5 species)
IV. *Comaropsis* F. (2 species)

V. *Cylactis* F. (14 species)
VI. *Orobatus* F. (19 species)
VII. *Dalibardastrum* F. (4 species)
VIII. *Malachobatus* F. (114 species)
IX. *Anoplobatus* F. (6 species)
X. *Idaeobatus* F. (117 species)
XI. *Lampobatus* F. (10 species)
XII. *Eubatus* F. (number unknown, Focke ± 135)

Of these the 3 most important groups (*Malachobatus*, *Idaeobatus* and *Eubatus*) have each a well defined area of distribution: the subgenus *Malachobatus* is confined to S.E. Asia (Japan, Malayan Archipelago), Australia and Madagascar; the *Idaeobati* are having their chief area of distribution slightly more to the North, viz. in China, Japan and the E. Himalaya, but also in E. and S. Africa, while *R. Idaeus*, the type species of the group, has a circumpolar distribution. The *Eubati* have their richest centre of development in S. America, although one of their subdivisions, the *Moriferi*, occurs in Europe, where it is divided

MORIFERI Focke (1874)

W. O. Focke (1903) in: Aschers.&Graebner, Syn. Bd. IV, 1e Abt.	W. O. Focke (1914) in: "Species Ruborum"	H. Sudre (1913) in: "Rubi Europae"
15. groups:	4 subsections, 16 series	5 sections, 13 subsections and 13 series
1. *Suberecti*	Subsectio: *Suberecti*	A. *Homalacanthi*
2. *Rhamnifolii*	I. *Suberecti* veri	Sectio I: *Suberecti*
3. *Candicantes*	II. Appendix ad Suberectos	Sectio II: *Silvatici*
4. *Tomentosi*	A. Series *Properi*	Subsectio a: *Grati*
5. *Discolores*	B. Series *Semi-Suberecti*	series: *Eu-grati*
6. *Silvatici*	Subsectio: *Senticosi*	series: *Sprengeliani*
7. *Sprengeliani*	I. *Rhamnifolii*	Subsectio: b *Euvirescentes*
8. *Egregii*	II. *Tomentosi*	series: *Calvescentes*
9. *Grandifolii*	III. *Thyrsoidei*	series: *Piletosi*
10. *Vestiti*	IV. *Discolores*	series: *Nemorensis*
11. *Radulae*	V. *Silvatici*	Subsectio c: *Discolores*
12. *Apiculati*	VI. *Egregii*	series: *Subvirescentes*
13. *Koehleriani*	VII. *Vestiti*	series: *Subdiscolores*
14. *Glandulosi*	VIII. *Grandifolii*	series: *Imbricati*
15. *Corylifolii*	IX. *Radulae*	Sectio III: *Discolores*
	Subsectio: *Glandulosi*	Subsectio a: *Subvirescentes*
	I. *Koehleriani*	Subsectio b: *Hedycarpi*
	II. *Eu-Glandulosi*	Subsectio c: *Candicantes*
	Subsectio: *Caesii*	Subsectio d: *Subtomentosi*
	I. *Caesii veri*	B. *Heteracanthi*
	II. *Corylifolii*	Sectio IV: *Appendiculati*
		Subsectio a: *Tomentosi*
		Subsectio b: *Vestiti*
		series: *Hypoleuci*
		series: *Virescentes*
		series: *Hebecaules*
		Subsectio c: *Radulae*
		series: *Micantes*
		series: *Concolores*
		Subsectio d: *Rudes*
		Subsectio e: *Hystrices*
		Subsectio f: *Glandulosi*
		Sectio V: *Triviales*

into an enormous number of forms. The *Eubati* are lacking completely in the regio round the Pacific and Indian Ocean.

The *Eubati*, the group to which also our brambles belong, are divided by Focke into 6 sections: *Xerocarpi*, *Ursini*, *Dissitiflori*, *Floribundi*, *Duri* and *Moriferi*; the last section represents our true brambles (brambles in a stricter sense). These sections comprise respectively 3, 1, 2, 24, 5 and ± 100 species. They are distributed on the American continent, Europe and N. Africa.

The further subdivision of the European *Moriferi* by Focke and Sudre is shown in the survey on the foregoing page.

Main species ("circle-species") of the *Moriferi* accepted by Gustafsson (1943) are shown in the following table[1]):

A. HOMALACANTHI Dum.

Subsectio: SUBERECTI Müll.:

R. nessensis W. Hall., *R. plicatus* Wh. et N., *R. fissus* Lindl., *R. sulcatus* Vest., *R. nitidus* Wh. et N., *R. affinis* Wh. et N.

Subsectio: SILVATICI Müll.:

Series: Grati Sudre:

R. carpinifolius Whe, *R. vulgaris* Wh. et N., *R. clethrophilus* Gen., *R. gratus* F., *R. chaerophilus* Sag. et Sch., *R. hypomalacus* F., *R. Arrhenii* Lange, *R. Sprengelii* Whe, *R. hesperius* Rog., *R. myricae* F., *R. chlorothyrsos* F.

Series: Euvirescentes Gen.

R. Questierii Lef. et Müll., *R. rhombifolius* Whe, *R. pyramidalis* Kalt., *R. macrophyllus* Wh. et N., *R. silvaticus* Wh. et N., *R. Gremlii* F., *R. egregius* F.

Series: Discoloroides Gen.

R. villicaulis Koehl., *R. argenteus* Wh. et N., *R. polyanthemus* Lindeb., *R. rhamnifolius* Wh. et N., *R. Bollei* F. (primary species), *R. canariensis* F., *R. Hochstetterorum* Seub.

Subsectio: DISCOLORES Müll.:

R. ulmifolius Schott (primary species), *R. Godronii* Lec. et Lmtt., *R. bifrons* Vest., *R. Lindebergii* Müll., *R. pubescens* Wh. et N., *R. geniculatus* Kaltenb., R. procerus Müll., *R. thyrsoideus* Wimm.

B. HETERACANTHI Dum.

Subsectio: APPENDICULATI Gen.:

Series: Tomentosi Wirtg.:

R. tomentosus Borkh. (primary species).

Series: Vestiti Focke:

R. vestitus Wh. et N., *R. Boraeanus* Gen., *R. adscitus* Gen., *R. mucronatus* Blox.

Series: Grandifolii Focke:

R. incanescens Bert. (primary species), *R. grandifolius* Lowe, *R. Steudneri* Schwnf. (primary species?).

Series: Radulae Focke:

R. radula Wh. et N., *R. Genevierii* Bor., *R. apiculatus* Wh. et N., *R. fuscus* Wh. et N., *R. foliosus* Wh. et N., *R. infestus* Wh. et N., *R. thyrsiflorus* Wh. et N., *R. pallidus* Wh. et N., *R. obscurus* Kalt., *R. Menkei* Wh. et N.

Series: Rudes Sudre:

R. melanoxylon Müll. et Wirtg., *R. rudis* Wh. et N., *R. vallisparsus* Sudre.

Series: Hystrices Focke:

R. fuscoater Wh. et N., *R. pilocarpus* Grl., *R. Lejeunei* Wh. et N., *R. rosaceus* Wh. et N., *R. hystrix* Wh. et N., *R. Koehleri* Wh. et N.

Series: Glandulosi Müll.:

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[1]) This survey is incomplete according to G. himself.

R. scaber Wh. et N., *R. Schleicheri* Wh. et N., *R. platyphyllos* Koch (primary species?), *R. moschus* Juz. (primary species), *R. Bellardii* Wh. et N., *R. serpens* Wh., *R. hirtus* Waldst. et Kit.

Subsectio: CAESII Focke:

R. caesius L. and the innumerable *Corylifolii.*

Finally, to give an idea of the number of main species, micro-species and varieties GUSTAFSSON (1943) has compiled from SUDRE's monograph the following list:

A. HOMALACANTHI Dum.

Subsect. I: *Suberecti* Müll.:	7	main species	19	micro-species	40	varieties
Subsect. II: *Silvatici* Müll.:	41	,,	160	,,	316	,,
Ser. a: *Grati* Sudre:	16	,,	57	,,	109	,,
Ser. b: *Euvirescentes* Gen:	14	,,	60	,,	107	,,
Ser. c: *Discoloroides* Gen:	11	,,	39	,,	100	,,
Subsectio III: *Discolores* Müll.:	11	,,	76	,,	244	,,
Ser. a: *Gypsocaulon* Müll.:	2	,,	28	,,	114	,,
Ser. b: *Hedycarpi* F.:	7	,,	26	,,	56	,,
Ser. c: *Candicantes* F.:	1	,,	13	,,	42	,,
Ser. d: *Subtomentosi* Sud.:	1	,,	9	,,	32	,,

B. HETERACANTHI Dum.

Subsectio IV: *Appendiculati* Gen.: 50 main species 440 micro-species 1327 varieties

Notwithstanding the fact that FOCKE and SUDRE have been working independently, in totally different regions of Europe, their systems show a fairly clear resemblance, in regard to the subdivision into groups as well as to the choice of main species ("circle-species").

Both systems are actually based on the old system of P. J. MÜLLER (1859) in which system already 6 groups, viz. *Suberecti*, *Discolores*, *Silvatici*, *Spectabiles*, *Glandulosi* and *Triviales* (= *Caesii*, incl. *Corylifolii*) were distinguished. Five of these groups are still in use, although as their delimitation has already shown, they did not all keep the same systematic value.

As to the main species, the following comparison has been made by GUSTAFSSON (1943, p. 28): "FOCKE listed in his monograph of 1914 as many as 73 important microspecies from Europe and North-Africa, each given a number of its own. Of these types eight are extra-European and therefore not dealt with by SUDRE. Of the remaining 65 types 52 are circle-species in SUDRE's manual and two are listed as circle-species under different names, i.e. 80—83 % of FOCKE's main types are regarded as such also by SUDRE. (It should be kept in mind, however, that the two batologists did not always delimit their "species" in the same manner). The thirteen main types handled in a different manner by the French botanist consist predominantly of English brambles, of which he evidently possessed but poor or at least incomplete information (see for instance the criticism in RIDDELSDELL's paper of 1923).

"Of SUDRE's 110 circle-species, on the other hand, 54 are identical and considered to be main types in FOCKE's monograph, 33 are regarded as "species" but given a lower taxonomic rank (not furnished with numbers of their own). Nine of SUDRE's circle-species are mentioned as unimportant or hybridogenous forms, and 14, finally, not even recognized by FOCKE. Thus 87 of 110 circle-species (= 79 %) are characterized as rather essential types by both authors." (G.)

From this it is clear that these two meritorious investigators have come to closely corresponding results. FOCKE has been studying the *Rubi* for an important part in nature, i.e. in the living condition. He was the first to distinguish the main species and to discuss their interrelationships. It was SUDRE who founded a well justified system and also excelled in the arrangement of forms of subordinate systematic rank.

However, FOCKE's descriptions are in many instances more detailed, so that their works are supplementing each other. SUDRE is the more generally used at present.

WATSON's system (1948) differs so much from the older ones that a comparison is difficult. It is moreover adapted especially to the English bramble flora.

SUMMARY

On the habit, ecology and taxonomy of the brambles of the Netherlands.

1. The connection between mode of life and taxonomic position of our *Rubus* species is discussed. The importance of the influence of environmental and heriditary factors on the habit and development of the plant is pointed out.
2. A knowledge of the mode of life and the behaviour of the plants in definite ecological conditions is of importance for recognizing the species in the field. A survey is given of the principal ecological data.
3. The various modes of multiplication are summarized, since they lead to a better understanding of the species and of the ecological forms mentioned above.
4. In conclusion the classification proposed for the genus *Rubus* by FOCKE and by SUDRE are reproduced and compared.

REFERENCES

BABINGTON, C. C. (1869). The British Rubi. London.

BABINTON, C. C. (1904). Manual of British Flora. 9th Edit. London.

CRANE, M. B. and DARLINGTON, C. D. (1927). The origin of new forms in Rubus. Genetica 9.

CRANE, M. B. and THOMAS, P. T. (1939). Segregation in asexual (apomictic) offspring in Rubus. Nature 143, p. 684.

CRANE, M. B. and LAWRENCE, W. J. C. (1952). The genetics of garden plants. 4th Edit. London.

DARROW, G. M. (1931). European blackberry seedlings and hybrids. Journ. Hered. 22.

DARROW, G. M. and LONGLEY, A. E. (1933). Cytology and breeding of Rubus macropetalus, the logan, and related blackberries. Journ. Agr. Res. 47.

DARROW, G. M. and WALDO, G. F. (1933). Pseudogamy in blackberry crosses. Journ. Hered. 22.

Focke, W. O. (1877). Synopsis Ruborum Germaniae. Bremen.

Focke, W. O. (1881). Die Pflanzenmischlinge. Berlin.

Focke, W. O. (1903). Rubus in Ascherson, P. und Graebner, P. Synopsis der mitteleuropäischen Flora, VI; 1. Leipzig.

Focke, W. O. (1910). Die Sternhärchen auf den Blattoberflächen der europäischen Brombeeren. Abh. Naturw. Ver. Bremen XX. 186.

Focke, W. O. (1910). Gelegentliche Hybriditätszeichen bei Brombeeren. Abh. Naturw. Ver. Bremen XX, 1.

Focke, W. O. (1911—1914). Species Ruborum. Monographiae generis Rubi Prodromus. I—III. Bibl. Botanica 17—19.

Fritsch, K. (1887). Anatomisch-systematische Studien über die Gattung Rubus. Sitz. Ber. Wiener Akad. Wiss. Bd. 95.

Gustafsson, Å. (1935). The importance of the apomicts for plant geography. Bot. Not. (Lund).

Gustafsson, Å. (1943). The genesis of the European Blackberry Flora. Lunds Univ. Årsskr. N. F. Avd. 2 Bd. 39, nr. 6.
(further literature of importance).

Gustaffson, Å. (1946). Apomixis in higher plants. I. Lunds Univ. Årsskr. N. F. Avd. 2, T. 42, no. 3, pp. 1—66.

Gustaffson, C. E. (1938). Skandinaviens Rubus-flora. Bot. Not. (Lund).

Heukels, H. en Wachter, W. H. (1934). Geïllustreerde Schoolflora voor Nederland. Groningen.

Keller, R. und Gams, H. (1922). Rubus, in: Hegi, Ill. Flora v. Mitteleuropa IV. 2. München.

Lindman, C. A. M. (1926). Svensk Fanerogamflora. Stockholm.

Lidforss, B. (1905—1907). Studier över artbildningen inom släktet Rubus. I—II. Ark. f. Bot. 4, 6.

Lidforss, B. (1907). Über das Studium polymorpher Gattungen. Bot. Not. (Lund).

Lidforss, B. (1914). Resumé seiner Arbeiten über Rubus. Zeits. ind. Abst. u. Vererb.lehre 12.

Longley, A. E. (1924). Cytological studies in the genus Rubus. Am. Journ. Bot. 11.

Müller, P. J. (1859). Versuch einer monographischen Darstellung der gallogermanischen Arten der Gattung Rubus. Jahresber. Pollichia-Neustadt.

Nordhagen, R. (1940). Norsk Flora. Oslo.

Perttula, U. (1941). Untersuchungen über die generative und vegetative Vermehrung der Blüthenpflanzen in der Wald-, Hain-, Wiesen- und Hainfelsenvegetation. Ann. Acad. Scient. Fenn. Ser. A. 58.

Riddelsdell, H. J. (1923). Sudre's Rubi Europae. Journ. of Botany, 61.

Rogers, W. M. (1900). Handbook of British Rubi. London.

Sudre, H. (1908—1913). Rubi Europae. Paris.

Sudre, H. (1913). Bréviaire du Batologue ou Analyse descriptive des Ronces d'Europe. Paris.

Schinz, H. und Keller, R. (1905). Flora der Schweiz. I—II. 2e Aufl. Zürich.

Weihe, K. E. et Nees von Esenbeck, C. G. (1822—1827). Rubi Germanici. Elberfeld.

Winge, O. (1938). The genetic aspect of the species problem. Proc. Linn. Soc. London. Session.

Watson, W. (1946). List of British species of Rubus, and key to sections, subsections and series of Eubatus. Journ. of Ecology, 33, pp. 337—344.

Watson, W. (1948). An introduction to the study of Rubus. In: British flowering plants and modern systematic methods. Rep. Bot. Soc. Brit. Isles.

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ZUR DATIERUNG EINER MOORLEICHE

VON

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(*Eingegangen 25. Sept. 1952*)

In Dezember 1951 wurde in einem kleinen Moor nordwestlich von Zweeloo (Prov. Drenthe) bei Urbarmachungsarbeiten eine Moorleiche gefunden. Wie öfters war auch diese Leiche stark verletzt worden, da man zu spät gemerkt hatte, dass man es mit dem Leichnam eines Menschen zu tun hatte. An der Fundstelle der Moorleiche betrug die Mächtigkeit des Moores 60 cm und der Untergrund war aus feinkörnigem Sand zusammengesetzt. In einer Tiefe von 30 cm war ein sehr ausgeprägter Uebergang vom stark zersetzten, braunschwarzen Torf zum wenig humifizierten, hellbraunen, jüngeren *Sphagnum*torf zu beobachten (Grenzhorizont). Von dem Torf wurde eine Anzahl Proben entnommen. Nach den Angaben der Arbeiter hatte man die Leiche in einer Tiefe von ungefähr 45 cm, also in dem schwarzen Torf gefunden.

Die Reste der Moorleiche sind in dem Anatomisch-Embryologischen Laboratorium der Universität in Groningen untersucht worden, wobei sich herausstellte, dass diese einer jungen, etwa 170 cm grossen Frau zugehört haben.

Für das Pollendiagramm ist die für holocene Diagramme übliche Darstellungsweise benutzt worden. Die Prozentsätze der Kräuter, Farne und Moose sind bezogen auf die Baumpollensumme, in welcher *Corylus* mit einbegriffen ist (FAEGRI & IVERSEN 1950, JONKER 1952).

Die unterste Probe zeigt ein sehr deutliches präboreales Spektrum: *Betula* hat einen sehr hohen Wert, während von den wärmeliebenden Bäumen nur *Corylus* anwesend ist. Auffallend in dieser Probe ist nebst vielen Sporen von *Equisetum* (150 %) die grosse Anzahl von *Myriophyllum*pollen (34 %). In der nächsten Probe (Tiefe 51 cm) erscheinen die Erle (*Alnus*) und die Eiche (*Quercus*), so dass diese Probe wohl der borealen Zeit entspricht. Von den wichtigsten Wasserpflanzen sind noch zu erwähnen: *Comarum palustre*, *Filipendula Ulmaria*, *Menyanthes trifoliata* und eine *Umbellifere*, sehr wahrscheinlich vom Genus *Oenanthe*.

Auf dieser frühholocenen Moorablagerung folgt eine deutliche Lücke und fängt das Moorwachstum erst wieder im Subboreal an. Ein ähnlicher Hiatus ist auch von SCHUETRUMPF (JANKUHN & SCHUETRUMPF 1952) in dem Thorsberger Moor (Schleswig-Holstein) festgestellt worden: das Moorwachstum hört im Anfang des Boreals auf und die Torfbildung beginnt wieder im Subboreal.

Der subboreale Teil dieses Diagrammes stimmt überein mit den entsprechenden Diagrammabschnitten der kleinen drenther Moore, die von Brouwer (1947) untersucht worden sind. Die Buche (*Fagus*) und die Hainbuche (*Carpinus*) kommen in niedrigen Prozentsätzen vor, während die Werte für *Alnus* nicht so hoch sind wie gewöhnlich. Auffallend ist das häufige Vorkommen vom Kiefer (*Pinus*).

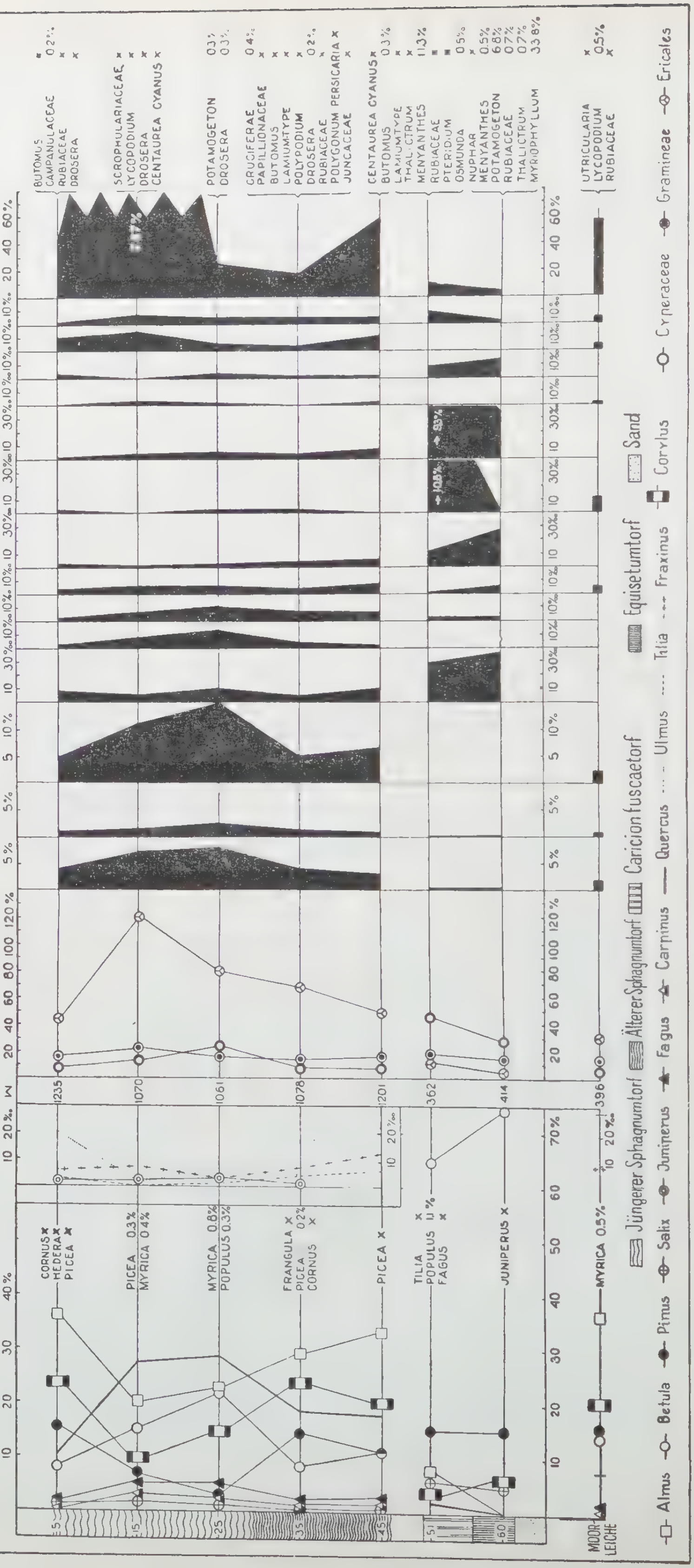
In dem stark zersetzten, älteren *Sphagnum*torf waren nebst Blattresten von *Sphagnum cuspidatum* auch Reste von *Carex*würzelchen und Blätter von *Drepanoclades* zu erkennen. Ausserdem gab es noch Reste von *Sphagnum magellanicum* und von Heide in dem oberen Teil des älteren *Sphagnum*torfes. In dem stark zersetzten Torf wurden ziemlich viele Sandteilchen gefunden.

Auch der subatlantische Diagrammabschnitt (der wenig humifizierte, jüngere *Sphagnum*torf über dem Grenzhorizont) gibt wenig Besonderheiten. Die Buche erreicht einen etwas höheren Prozentsatz, obwohl dieser noch ziemlich niedrig bleibt. Wahrscheinlich waren die Standortsbedingungen für diesen Baum in der Umgebung des Moores nicht besonders günstig (eine ausfürlichere Besprechung über diesen Gegenstand gibt Waterbolk 1947). Erwähnung verdient das Vorkommen von *Juniperus*pollen, was mit den hohen Werten für *Ericaceae* übereinstimmt. Da der *Juniperus*pollen unterrepresentiert ist (Van der Hammen 1951), ist es nicht verwunderlich, dass der Pollen des Wachholders in solchen niedrigen Prozentsätzen vertreten ist. Nur einmal wurde ein Pollenkorn von *Hedera* gezählt.

Das Wachstum des jüngeren Sphagnetums fing an mit *Sphagnum cuspidatum*. In diesem Torf wurden Würzelchen von *Carex* und *Eriophorum* gefunden nebst einigen vereinzelten Resten von *Calluna*. Mehr nach oben war *Sphagnum magellanicum* der wichtigste Torfbilder.

Es ist interessant, dass die Landnahme, wie diese zum ersten Mal in Dänemark von Iversen (1941) ausgearbeitet worden ist, in diesem Diagramm auch wieder sehr deutlich zum Ausdruck kommt. Von verschiedenen Unkräutern wie *Urtica*, *Artemisia*, *Plantago* und *Rumex* kommt sehr regelmässig Blütenstaub in den untersuchten Proben vor; *Rumex* erreicht sogar einen ziemlich hohen Prozentsatz. Auch gab es eine bedeutende Anzahl von Getreidepollen. In einer Tiefe von 25 cm zeigt der Unkräuterpollen ein Maximum. Man darf darum die Annahme machen, dass damals sehr in der Nähe des Moores der Boden kultiviert wurde. Nach dem Verlassen des nach einigen Jahren erschöpften Bodens war es die Birke, die als erster Baum den Boden wieder in Besitz nahm. Nach dieser Betulaphase konnte dann eine mehr oder weniger vollständige Regeneration des Waldes folgen. Es ist aber wohl sicher, dass oft die Regeneration des Waldes unterblieb und eine Heide entstand. Damit in Uebereinstimmung steht das Heidemaximum in 15 cm Tiefe. Dieses Maximum ist nur recht niedrig wenn man es mit den von Florschuetz & Wassink (1941) und von Brouwer (1947) gefundenen Maxima in sonstigen drenther Moorchen vergleicht. Die Umgebung unseres Moores war also wahrscheinlich nicht so stark verheidet wie bei den oben erwähnten

KLEINES HOCHMOOR BEI ZWEELOO (PROV. DRENTHE)



Mooren. Da der Torf in dieser Tiefe fast keine makroskopische Reste von *Ericaceae* enthält, ist der hohe Prozentsatz von *Ericales*-pollen nicht zurückzuführen auf die Pollenproduktion von *Ericaceae*, die auf dem Moor wuchsen.

Ueber das Vorkommen eines Pollenkorns von *Centaurea Cyanus* in 15 und 45 cm Tiefe kann noch folgendes gesagt werden: obwohl diese Pflanze in den Pollendiagrammen von Dänemark und Nordwestdeutschland im Allgemeinen erst nach 1300 vorkommt (MIKKELSEN 1949, SCHMITZ 1951), wird der Kornblumenpollen auch wohl vereinzelt schon in früheren Zeiten gefunden. SCHMITZ (1951) fand einige Pollenkörner in der Höhe des Grenzhorizontes, während TROELS-SMITH (1942) Kornblumenpollen in einigen Moorproben aus dem Ende der Bronzezeit (etwa 500 v. Chr. Geb.) gefunden hat.

Da man, wie oben erwähnt, die Moorleiche schon ausgegraben hatte, war die Oberfläche mit auf dem Moor liegenden, jüngeren *Sphagnum*torfresten verunreinigt worden und war es nicht einfach der Leiche eine zuverlässige Probe zu entnehmen. Nur der zwischen den Zehen des unverletzten Fusses befindliche Torf kam uns genügend zuverlässig vor. Leider war die Menge so gering, dass es nicht möglich war eine gleichgrosse Anzahl Pollenkörner auszuzählen wie bei den anderen subborealen und subatlantischen Proben. Das Ergebnis dieser Analyse ist an der Unterseite des Diagrammes wiedergegeben. Die Buche (*Fagus*) und die Hainbuche (*Carpinus*) sind vertreten, wenn auch in niedrigen Prozentsätzen, ebenso die Esche (*Fraxinus*) und die Ulme (*Ulmus*). Die Erle hat den höchsten Prozentsatz. In dieser Probe gibt es ziemlich viel Pollen von Getreide und Unkräutern, wie Sauerampfer (*Rumex*), Wegerich (*Plantago*) und Brennessel (*Urtica*). Vergleicht man die Analyse der Moorleichenprobe mit dem Diagramm, dann gibt es theoretisch zwei Möglichkeiten diese Probe in das Diagramm einzuordnen, nämlich etwas unter 45 cm Tiefe oder über 5 cm Tiefe. Für beide Fälle stimmen die Prozentsätze für *Alnus* und *Corylus* genau, während die anderen Baumpollen eine ziemlich gute Uebereinstimmung aufweisen. Die letzte Möglichkeit aber darf man ohne weiteres ausschalten, weil der Torf, der der Leiche entnommen wurde, stark zersetzter, älterer *Sphagnum*torf war und man nach Angaben der Arbeiter die Leiche in dem schwarzen Torf gefunden hatte. Aus diesen Gründen ist es wohl sicher, dass die Frauenleiche aus der Zeit am Ende der Schwarztorfbildung datiert.

Ohne die Fragen der Zeitstellung des Grenzhorizontes hier zu besprechen, darf man auf Grund der Untersuchungen von VAN GIFFEN (1947) und WATERBOLK (1950) den Anfang des Wachstums des jüngeren, ombrogenen *Sphagnum*torfes in den kleinen drenther Mooren ca Anfang fünftes Jahrhunderts nach Christi Geburt stellen. Und obwohl es nicht sicher ist, wieviel Zeit zwischen dem Aufhören des Wachstums des älteren und dem Anfang des jüngeren *Sphagnum*torfes liegt, weisen die Kurven der Baum- und Kräuterpollen darauf hin, dass es keine lange Zeit gewesen sein kann. Beim Uebergang vom stark zum wenig zersetzten *Sphagnum*torf zeigen die Kurven nämlich keine plötzlichen Aenderungen. Es ist darum wahrscheinlich, dass die betreffende Frau etwa im Anfang unserer Zeitrechnung gelebt hat.

In Uebereinstimmung hiermit steht die Tatsache, dass in dem Darm viele Schalen von Hirse (*Panicum miliaceum*) gefunden wurden. Nun war während der Periode von ± 500 v. Chr. Geb. bis in die römische Kaiserzeit die Hirse eine oft benutzte Nahrung (mündl. Mitt. Van Giffen). An den Gefässen aus dieser Zeit findet man mehrmals verkohlte Hirsekörner. Auch Netolitzky (1936) fand in dem Darm einer Moorleiche aus Drenthe, die ebenfalls aus dieser Zeit stammt, nebst Gerstenmehl die Schalen von *Panicum miliaceum*.

Zusammenfassend kann man sagen, dass die gefundenen Tatsachen, nämlich die Lage der Leiche im Torf, das Ergebnis der Pollenanalyse und das Vorkommen von Hirse in dem Darm, darauf hinweisen, dass die Frau etwa im Anfang des ersten nachchristlichen Jahrtausends gelebt hat.

LITERATURVERZEICHNIS

Brouwer, A. (1947),Pollenanalytisch onderzoek van overstoven Drentse veentjes. Tijdschr. Kon. Ned. Aardr. Gen. 64, 1—12.

Florschuetz, F. und E. C. Wassink (1941), Untersuchungen an niederländischen Mooren. L. Ergebnisse der Untersuchung einiger kleinen Moore im drenther Heidegebiet; ein Beitrag zur Lösung der Heidefrage. Rec. d. trav. bot. néerl. 38, 1—17.

Faegri, K. and J. Iversen (1950), Textbook of modern Pollenanalysis. Copenhagen.

Giffen, A. E. van (1947), Oudheidkundige perspectieven. Oudheidkundig Bodemonderzoek in Nederland (Gedenkboek Van Giffen), 497—544.

Hammen, Th. van der (1951), Late-glacial flora and periglacial phenomena in the Netherlands. Diss. Leiden.

Iversen, J. (1941), Landnam i Danmarks Stenalder. Danm. Geol. Unders. II. Raekke Nr. 66.

Jonker, F. P. (1952), A Plea for the Standardization of Pollen Diagrams. Taxon 1, 89—91.

Jankuhn, H. und R. Schuetrumpf (1952), Siedlungsgeschichte und Pollenanalyse in Angeln. Offa 10, 28—45.

Mikkelsen, V. M. (1949), Praestø Fjord. The development of the post-glacial vegetation and a contribution to the history of the Baltic Sea. Dansk Bot. Arkiv 13, 7—171.

Netolitzky, F. (1936), Speisereste in einer Moorleiche. Forschungen und Fortschritte 12, 269—270.

Schmitz, H. (1951), Die Zeitstellung der Buchenausbreitung in Schleswig-Holstein. Forstwiss. Centralbl. 70, 193—203.

Troels-Smith, J. (1942), Pollenanalytische Datierung zweier Pflüge vom Walletypus. Acta Archaeologica 13, 269—272.

Waterbolk, H. Tj. (1947), De oudheidkundige verschijnselen in verband met de ontwikkeling van plantengroei en klimaat. Oudheidkundig Bodemonderzoek in Nederland (Gedenkboek Van Giffen), 57—97.

Waterbolk, H. Tj. (1950), Palynologisch onderzoek van de versterking bij het Witteveen en de cultuursporen in het Bolleveen, beide bij Zeyen, gem. Vries. Nieuwe Drentse Volksalm. 68, 100—121.

A STUDY OF OXIDATION-REDUCTION POTENTIALS IN RELATION TO THE FUNCTIONS OF LIGHT AND CARBON DIOXIDE IN CHLORELLA PHOTOSYNTHESIS

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I. INTRODUCTION

It is now generally agreed that the process of photosynthesis involves the formation by the action of light and chlorophyll of chemical agents capable of reducing certain intermediates formed in non-photochemical reactions from carbon dioxide. It has been shown, moreover, that in partial systems such as isolated chloroplasts, illumination may result in the reduction of added compounds. As such, compounds of trivalent iron (1), quinones (2, 3), dyes (4, 5), some organic compounds (6) and pyridine nucleotides (7, 8) have been employed. This reduction is accompanied by the evolution of molecular oxygen, and may give rise to the formation of hydrogen peroxide (9).

It is likely that the reactions starting with the photochemical process proper, and leading to reduction of transformation products of carbon dioxide on the one hand, and to production of oxygen on the other hand, will involve one or more steps of coupled oxido-reduction (10). Some of the intermediates in these oxido-reduction chains may react with soluble compounds able to penetrate the cell wall. It would then be possible to demonstrate the occurrence of such compounds by means of potentiometric methods. We have therefore undertaken a study of the changes of the oxidation-reduction potential upon illumination of suspensions of green cells.

Several authors (l.c.) have studied the reduction of dyes by chloroplast suspensions. As has been confirmed by the work of WESSELS *et al.* (5) this is essentially equivalent to a colorimetric determination of the oxidation-reduction potential and the same end could be achieved by direct potentiometric measurement with the platinum electrode as has been reported by Spikes *et al.* (11). Perhaps the first to study oxidation-reduction potentials in suspensions of whole cells were TANG and LIN (12). In the light of present knowledge, their findings are no longer of great importance, however. The systematic use of the platinum electrode for potential measurements in suspensions of photosynthesising cells was initiated by WASSINK (13, 14) in a study of *Chromatium* photosynthesis. For various reasons we have considered it of interest to extend this work to the study of green non-anaerobic organisms. This has necessitated the development of some special methods, which will be described below.

II. EXPERIMENTAL METHODS

Special Warburg manometer vessels were developed to make possible the simultaneous measurement of gas exchange, oxidation-reduction potential and pH. (Fig. 1). In view of the necessity to accomodate a relatively large number of side-tubes as well as a sufficiently large inner vessel for gas absorption solutions, the total volume of the manometer vessel had to be rather large viz. about 80–100 ml. To prevent electrical leaks between the suspension in the vessel and the water in the thermostat via the joints, these were provided with glass collars protruding above the water level in the thermostat.

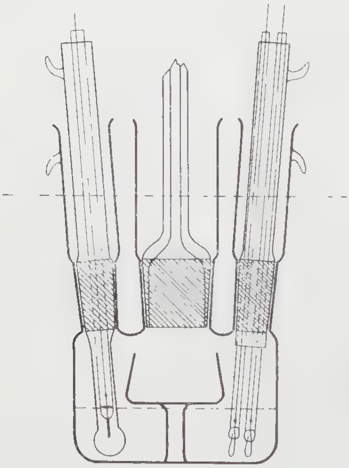


Fig. 1. Diagram of manometer vessel adapted to the measurement of pH and oxidation-reduction potential.

Great care is necessary in the use and treatment of the platinum electrodes. It is by no means easy to maintain a number of electrodes in such a condition that they indicate the same potential if submerged into the same suspension of algae, and that they keep their properties during a large number of experiments. We therefore had to devote special attention to the preparation and treatment of the electrodes. It was first found that properly prepared new electrodes, made from pure platinum wire indicated the same potential if put together in the same suspension, but that after a relatively small number of experiments deviations began to occur which eventually amounted to as much as 200 mV or even more. Originally we expected that the electrodes could be tested by putting them in a redox-mixture of predetermined potential. It was observed, however, that even badly "spoiled" electrodes (as judged from the potential reading in algal suspensions) indicated the expected potential to within 1 mV if immersed in a buffered saturated quinhydrone solution. This solution could be diluted 1000 to 10000 times before significant deviations occurred, and those were then in the same direction as found in the suspensions of algae. It is perhaps advisable to stress at this point the fact that the concentration of the redox systems excreted by living cells usually is so extremely small that minute differences in the individual properties of the electrodes become observable and behave as deviations from the ideal „inert" electrode. Earlier investigators (15) have attempted to overcome some of the difficulties inherent to this situation by adding small amounts of certain redox dyes to their solutions. After a certain period these compounds may assume the same potential as the systems excreted by the cells. They then greatly increase the poising capacity of the solution. This in turn improves the response of the electrodes. For reasons to be outlined elsewhere in this article, such a method could not be followed in the present investigation.

Finally the following method of preparing and cleaning the electrodes was adopted and gave quite reliable results. Pieces of clean platinum wire, 2 cm long and 0.2 mm in thickness were welded to the ends of 0.6 mm copper wire in an ethanol-oxygen flame containing excess ethanol. The platinum was folded to make a loop and then cleaned in chromic acid and washed in destilled water. A bead of lead glass was molten around the platinum wire just below the weld. This was performed in an ethanol-oxygen flame containing excess oxygen. Care is required not to melt the platinum at this stage. The electrode was then sealed on to the end of a soda glass capillary with an internal diameter of about 1 mm. The soda glass should be sealed to the lead glass only and should not touch the platinum. The glass tube served as a hold and as an electrical insulation for the copper wire. The use of lead glass as a transition glass, though not recommended by some authors, was found necessary to prevent the development of troublesome cracks, which are not always easily detected but may lead to completely erroneous potential readings. There is no objection against the use of lead glass provided care is taken during sealing operations to avoid blackening of the glass. The bead should stay perfectly clear and colourless.

Such freshly prepared electrodes worked quite well, but deteriorated quickly if no special precautions were taken. The deposition of tenaciously adhering grease films on the platinum surface is probably the chief though not the only cause for this effect. The presence of greasy materials is not to be excluded completely in media of biological origin. Therefore, at the conclusion of each experiment the electrodes plus the supporting glass tubes were cleaned by immersion in warm (90° C) chromic-sulfuric acid mixture for 2 min. Before a new experiment was started this procedure was always repeated. If the electrodes are now used at this point, the potential readings usually are completely erroneous. It may be that the platinum has become saturated with oxygen and that it takes a long time before this is removed completely. In order to bring the platinum in a suitable and reproducible condition again, we have put the electrodes after the chromic acid treatment in sets of three together in a 1N KOH solution and subjected them to an electrolytic treatment. The electrodes are first connected to the positive terminal of a 6 volts battery, another Pt-wire serving as the opposite electrode. After one minute electrolysis the direction of the current is reversed and the electrodes then electrolysed for another 2 min. at the negative pole. To remove the excess hydrogen now present on the electrodes, they are immersed after careful washing in a solution of methylene blue 1 : 10^6 containing some alkylsulfonate-type detergent. After 15 min. exposure to this solution the electrodes were very carefully washed with destilled water to remove all possible traces of methylene blue and then used immediately. We carefully checked this cleaning method and those tried, before the method was adopted definitely, by comparing such electrodes with freshly prepared non-treated electrodes in the same algal suspension. The electrodes treated in the way described above were found to indicate exactly the same potential as the fresh electrodes. The only difference is that after having been in use for some time the treated electrodes reach the final potential more quickly than fresh ones so that evidently the treatment "improves" the response. The usefull life of electrodes treated in this way varies somewhat, but may be of the order of 100–200 hours actual service. Notwithstanding the cleaning treatment this period is restricted and we have not been able to find a method keeping the electrodes in perfect condition indefinitely. In order to check the electrodes, three of them were always used together in one experiment. To this end, three electrodes were sealed into one ground joint cone with sealing wax. Very good electrodes agree to within one millivolt. As soon as the readings of the separate electrodes begin to differ by more than 30 mV we put in one new electrode. If the differences are found persistent we replace the whole lot. The agreement between the individual electrodes is least during rapid changes in the potential and there appear to be unavoidable differences in the speed of response even between otherwise very good electrodes. Bad ones often also assume the right potential if kept in the suspension for a very long time.

Between experiments the electrodes are kept immersed in destilled water.

The use of a glass electrode in the vessels is often convenient though not normally essential in buffered suspensions.

One of the joints on the manometer vessels takes a glass capillary filled with 1N KCl-agar. These capillaries are connected by means of rubber tubing to the same reservoir filled with saturated KCl solution in which the saturated calomel half cell is placed. The various electrodes can be connected separately to the electrometer (Coleman model 3D) by means of shielded polythene-insulated cables.

In most experiments, oxygen-free gas atmospheres were used. They were prepared by passing either nitrogen or nitrogen with 5 % carbon dioxide, taken from steel cylinders, over copper gauze heated electrically to about 450° C. In the case of nitrogen the gas also passes through two gas-washing bottles containing a 20 % solution of KOH and through a soda-lime tube.

In some experiments the center well in the manometer vessel contained solutions for the removal of specific constituents from the gas atmosphere. For removing carbon dioxide, one half ml. of a 20 % solution of KOH was used. If we wanted to remove oxygen as well we added to this liquid one half ml. of a 10 % pyrogallol solution. For removing oxygen in the presence of carbon dioxide we used 1 ml of a chromous sulfate solution. This was prepared by reducing a saturated solution of potassium chrome alum acidified with sulfuric acid by means of amalgamated zinc turnings until the colour of the solution was clear blue. The oxygen absorbing capacity of this solution is not very large, however, and 1 ml usually suffices for a short time only to absorb the oxygen evolved during normal photosynthesis with the amounts of algae used in our experiments. All the oxygen absorbing solutions were added to the center well after flushing the manometer vessels with the oxygen-free gasses.

In the pH interval 6–8 use was made of M/15 phosphate buffers acc. to Sörensen. Between pH 5 and 6 we used M/15 phthalate buffers or mixtures being M/15 in phthalate and M/30 in phosphate.

In some experiments we wanted to add substances to the suspensions during the course of the experiment. Some of our vessels were provided with the usual type of side bulb for this purpose. As the addition of liquid from this side arm to the main compartment involves tilting of the manometer with concomitant temporary interruption of shaking and decrease in illuminating intensity, we have found it advisable as a rule to follow a different method. Thin-walled glass bulbs were blown at the end of capillary tubes. The bulbs were filled with the solutions to be added and the capillaries were sealed. The liquids were usually freed from oxygen and care was taken to fill the bulbs completely. They were inserted into the manometer vessels with a glass rod passing through a rubber stopper which was placed in one of the side arms of the vessel. The bulbs could easily be broken at any desired time during an experiment by simply pushing down the supporting rod until the bulb shattered against the bottom of the vessel. The amount of liquid could be determined very accurately by weighing.

The manometer vessels could be illuminated in the usual way from the bottom by means of two Philips' SO 1000 sodium vapour lamps. The light was filtered through 1 cm of a 5 % copper sulphate solution to remove the infra red radiation. The maximum incident intensity obtained in this way was about 4×10^4 erg/cm^2 sec. Lower light intensities were obtained with the aid of glass filters. The light intensities were measured at the place of each vessel with a calibrated Moll thermopile immersed in the thermostat bath and connected to a galvanometer.

The algae used in this investigation were cultivated from a strain of *Chlorella vulgaris* usually employed in this laboratory. They were grown for 3–4 days in Warburg's medium (16) with fluorescent tubes as the light source. In a few experiments we used a strain of *Scenedesmus quadricauda* isolated by the author. This organism was cultivated in the same way as the strain of *Chlorella.* At the start of the experiments the algae were centrifuged and resuspended in the desired buffer to a density of 4 mm^3 wet cells per ml. It is not advisable to use much more dilute suspensions as the potential readings then tend to become erroneous. From this point of view a more concentrated suspension would have been preferable but this would have made the average light intensity in the suspension rather low.

Potential values reported in this paper are quoted as measured against the saturated calomel half cell.

III. RESULTS

a. Role of oxygen and hydrogen peroxide

At an early stage of our experiments it was realised that in green organisms the potential behaviour is complicated by the fact that in air respiratory processes are possible which may also contribute to the potential formation. As a matter of fact, if the experiments are conducted in air a stable potential is set up in the dark at a rather high level and there is hardly any change upon illumination. Even in nitrogen containing only 2 % oxygen there is practically no reaction upon illumination (fig. 2 upper curve). On the other hand, if a suspension of algae at pH 7 is illuminated in complete absence of carbon dioxide and oxygen, illumination produces a marked change in the oxidation-reduction potential (fig. 2, lower curve). Similar experiments can be done in gas mixtures containing carbon dioxide. In this case we have observed that the production of oxygen during the illumination does not influence the potential values but that the oxygen formed influences the dark potential set up after the suspension is put in the dark again. In fig. 2 two such experiments are given also (indicated with "$N_2 + 5\ \%\ CO_2$"). In one of these a sufficient amount of chromous solution was added to the center well to absorb all the oxygen produced during illumination, in the other the chromous

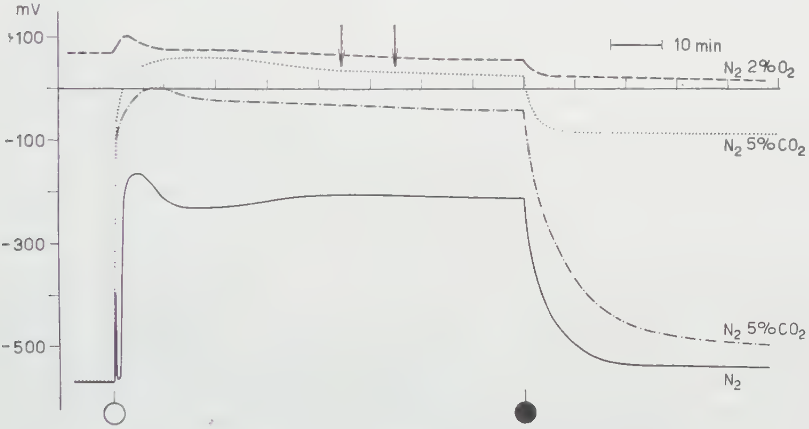


Fig. 2. Influence of oxygen upon the potentials.

———— Gas phase pure nitrogen. Center vessel with alkaline pyrogallol.

- - - - - - - Gas phase nitrogen plus 2 % oxygen.

—.—.—. Gas phase nitrogen plus 5 % carbon dioxide. Center vessel with chromous solution.

Gas phase nitrogen plus 5 % carbon dioxide. Center vessel with chromous solution which became saturated with oxygen during the time interval, indicated by the arrows.

In this and the subsequent figure s, ○ indicates the moment the light was turned on, ● the moment the light was turned off.

solution became saturated during the time interval indicated by the arrows. This could be followed accurately by observing the manometer readings which change sign as soon as the oxygen is no longer absorbed. The difference in dark level is very pronounced though there is little difference in potential in the light. It appears therefore, and more experiments of the same type have convinced us, that the potential level in the dark (DP) is strongly dependent upon the presence of oxygen. This is doubtlessly due to respiratory processes. At a sufficiently high concentration of oxygen this effect completely supersedes the effects of the illumination. For this reason we have considered it necessary to conduct most of our further experiments in the absolute absence of oxygen. More detailed examples of the potential changes upon illumination of anaerobic suspensions are given in the following figures (e.g. fig. 7) and will be discussed in a later section.

Two questions now arise. The first is: what mechanism is responsible for the establishment of the anaerobic dark potential? We will discuss this point later. The second is of fundamental importance for the interpretation of the experiments, described in this paper. It appears that, at least at pH 7, the ultimate effect of illumination in the absence of air is a considerable rise in potential (fig. 2). Is this rise due to the production of oxygen? It is known that even in the absence of carbon dioxide small amounts of oxygen are formed from intracellular hydrogen donors.

The argumentation will be divided in two sections viz. one applying to the presence of carbon dioxide, the other to the absence of it. In the experiments illustrated in fig. 2, we have studied the effect of complete and partial removal of photosynthetically produced oxygen. It will be clear, that from the moment on indicated by the arrows a quite considerable amount of oxygen collected in the gas phase and this was observable both from the manometer readings and from the subsequent potential in the dark. Notwithstanding this the potential in the light (LP) does not show any influence of this oxygen-accumulation as evidenced by a comparison with a similar experiment, where the oxygen was removed rigorously throughout the illumination period. These results do not give support to the theory that oxygen is directly responsible for the rise in potential during illumination in the presence of carbon dioxide.

We will now consider the experiments in the absence of carbon dioxide (fig. 3). After the establishment of a stationary DP, in one experiment nitrogen with 0.2 % oxygen was passed through a vessel at moment *a*. The amount of oxygen present in that vessel thereby increased from practically zero to about 150 mm^3. This was accompanied by a rise in the potential of 65 mV. During illumination in the absence of carbon dioxide the potential may rise as much as 450 mV and if oxygen production was responsible for it, much more than 150 mm^3 should therefore be constantly present in the manometer vessel during the final part of the illumination period. The limit of accuracy of the manometer readings corresponds to about

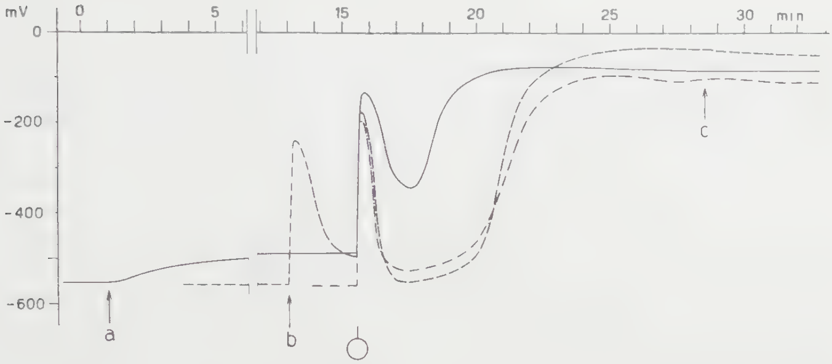


Fig. 3. Influence of oxygen. Three different vessels. At moment *a*, nitrogen plus 0.2 % oxygen was passed through the suspension. At *b*, a solution of 6 mm³ oxygen in water was added. At *c*, a solution of 0.25 mg catalase was added.

5 mm³. In experiments of this type we have never observed a gas production surpassing this quantity. Therefore, the large rise in potential during illumination cannot be explained by oxygen production. This conclusion is strongly supported by the results of other experiments where the oxygen pressure in the vessels was also kept constant, namely zero, by passing pure nitrogen through the vessels during the illumination period. This should effectively remove the oxygen or at least prevent a build-up in the gas phase. Nevertheless the potential course in this case is exactly the same as in a parallel experiment where no nitrogen is passed through the liquid. It appears superfluous, therefore, to give an illustration of such an experiment. Combining the evidence reported above it appears highly probable that the large rise in potential upon illumination both in the presence and absence of carbon dioxide is due to other causes than the production of oxygen. As will be shown in a later section, under certain conditions of pH the potential in the light is lower than in the dark and this is a confirmation of the conclusion arrived at above. The reasoning given here applies to the stationary LP only and the experiment *a* of fig. 3 shows that unlike in the stationary phase, oxygen has influence upon the induction phase of the potential. We will return to this point later on.

During the course of our investigations we became aware of a publication by Mehler (9) who has shown that in the absence of hydrogen acceptors, chloroplasts may use oxygen as a hydrogen acceptor during the Hill reaction, thereby forming hydrogen peroxide. On the basis of equivalent amount of oxygen, hydrogen peroxide is a much more powerful oxidising agent than molecular oxygen and it was therefore not to be excluded that in our case the observed potential rise was due to the production of small amounts of hydrogen peroxide. To test this possibility we have added to our algal suspensions an amount of catalase very much greater than the amount naturally occurring in the algae. In fig. 3. is illustrated an experiment in which the algae were illuminated under the usual conditions but where at the moment *c*, 0.25 mg cryst. catalase dissolved in phosphate buffer pH 7.0 was added. This did not influence the potential in any way. The same holds when the catalase is added before the start of illumination (experiment not illustrated). We therefore conclude that the potential in the stationary phase in the light is not related to the presence of hydrogen peroxide either.

An examination of the curves representing the potential changes in nitrogen at pH 7.0 reveals that there is a sudden "outburst" of an oxidising reaction during the first seconds of the illumination. A maximum is usually reached about 20 sec. after the start of the illumination. This is followed by a quick fall in potential to about the dark level after which a slower rise to the stationary level sets in. Usually there is another indistinct maximum before this final level is reached (e.g. in the lower curve of fig. 2) but this is not always very pronounced though seldom completely absent. The significance of the initial peak is not clear and the phenomenon does not occur at lower pH (section *b*). The following observation may have bearing upon the phenomenon. In experiment *b* of fig. 3 we have added at moment *b* to the suspension of algae in the dark about 6 mm^3 oxygen dissolved in water. There is a quick mixing of the oxygen with the solution and the potential rises immediately. At the same time the oxygen starts to equilibrate with the gas atmosphere so that the potential soon falls again. The general shape of this "oxygen peak" is very similar to the initial peak during illumination and it is not to be excluded that the last mentioned phenomenon is due to the sudden release of a small amount of oxygen. A similar peak can be found in the induction curve for chlorophyll fluorescence in *Chlorella* and this was supposed earlier by WASSINK *et al.* to be connected with oxygen liberation through the Hill reaction (33). More recently VAN DER VEEN (17) demonstrated such an "oxygen gush" in higher plants immediately after the start of illumination by a gas analytical method. As follows from the experiments to be discussed under section *e*, such a temporary oxygen production cannot be due to previous accumulation of carbon dioxide.

b. Influence of pH upon the potentials in the light and in the dark

Between pH 5 and 8 the hydrogen ion concentration of the suspension mainly affects the potentials in the dark and to a much smaller extent the potentials in the light. This applies equally to experiments with and without carbon dioxide. In fig. 4, the results of a number of observations are collected. Notwithstanding the fact that the behaviour of different batches of algae towards illumination is only qualitatively and never quantitatively the same, a circumstance which has been a serious limitation during our experiments, the DP's are remarkably reproducible. Between pH 6 and 8 (phosphate buffers) they follow a straight line with a slope of 60 mV per pH unit as is usual. There is a sudden sharp transition between pH 5.75 and 5.25. In this interval the slope is much too steep to be connected with phenomena of electrolytic dissociation (18) and we must conclude that in this region there is a change in the activity of some enzyme system connected with the metabolic reactions responsible for the establishment of the dark potential.

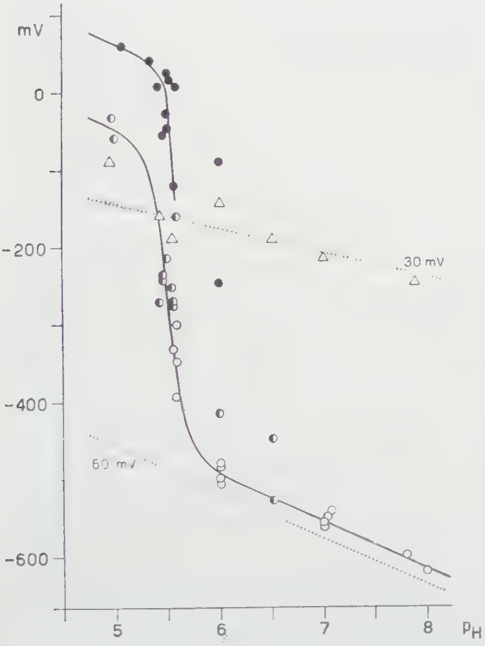


Fig. 4. The potentials as a function of pH. Dark potentials:

○ phosphate buffers.

◐ phosphate-phthalate buffers.

● phthalate buffers.

Potentials in the light (without carbon dioxide):

△ phosphate and phosphate-phthalate buffers.

In the region below pH 5.5 we have been using either phthalate buffer or a mixture of phthalate and phosphate buffers. As far as our observations go at present it appears that all buffers containing phosphate lead to DP's falling reasonably well on the same line. On the other hand the results with phthalate buffers are consistently higher by about 100 mV. As the observations with mixed buffers show, this is not due to a harmfull effect of the phthalate but must be ascribed to the absence of a sufficient concentration of phosphate. The phosphate effect is an interesting phenomenon in itself and we hope to be able to return to this matter in a later publication. Also in fig.4 have been given the points representing LP's in experiments without carbon dioxide. As will be treated in more detail under section *c*, the stationary potentials in the light are not very reproducible, depending upon a number of factors one of which is the previous anaerobic dark period. As much as possible we have collected in fig. 4 the results of experiments where the anaerobic dark period had been about 90 min. The potentials are those observed after 20-25 min. illumination and the values belonging to the same pH have been averaged. One thing is clear namely that the transition zone of the

DP's is not reflected in the LP's. The observed pH-dependency fits a 30 mV/pH line somewhat better than a 60 mV/pH line but the accuracy is insufficient to settle this question definitely.

It is evident that the mechanisms responsible for the establishment of the potential in the light, and in the dark are quite different and we must conclude that in first approximation they are entirely independent. Under anaerobic conditions in the dark there appears to be a certain metabolism leading to the production of reducing substances. It may be remarked here that our observations have confirmed the opinion expressed by other authors (17), that this anaerobic metabolism is also characterised by the production of a small amount of carbon dioxide (see section *e*).

The conclusion arrived at above is an important one as it emphasises the fact that no value is to be attached to a comparison of the potentials in the light with those in the dark. This also implies that during the first moments of the illumination there must be a transition from the dark metabolism to a metabolism in the light and though this is reflected in the potential changes, these are still influenced for a certain period by the preceding dark metabolism. If we now compare a number of induction curves at different pH such as are given in figs 5 and 6, we may conclude that after the first 20–30 seconds of the illumination the potential behaviour in the light is very similar even at widely different pH values. The experiments of figs 5 and 6 also show that the differences in DP's at the various pH values are not due to slowness in the attainment of a stationary potential level as the various potential curves return to their original level after the light is turned off again.

As follows from fig. 4 the stationary LP is higher than the DP above pH 5.5 in carbon dioxide-free media. Below this pH the reverse holds. This is illustrated by the results of the experiments shown in fig. 5. This observation appears to form an additional argument supporting the conclusion arrived at in section *a*, viz. that the potential changes in the light are not due to the evolution of oxygen or the

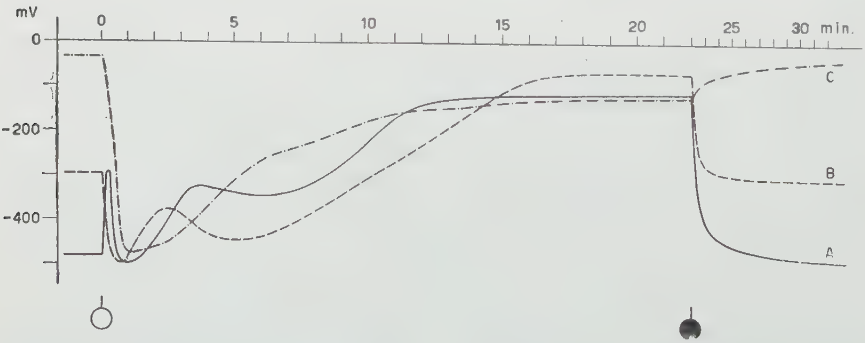


Fig. 5. Examples of potential curves at different pH and in different buffers. ——— Phosphate buffer pH 6.0. ------- Phosphate buffer pH 5.6. —.—.—. Phthalate buffer pH 5.5.

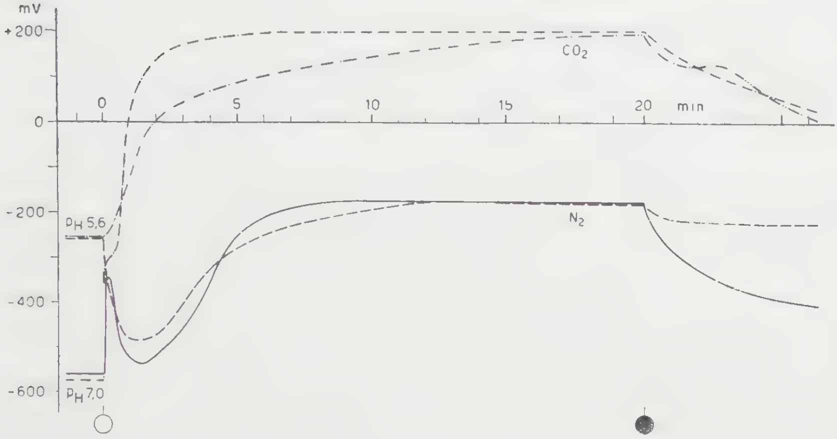


Fig. 6. Influence of the pH in the presence and absence of carbon dioxide.

production of hydrogen peroxide. Summarising the results discussed above we may say that the potential changes in carbon dioxide-free media during illumination are characterised by the attainment of a relatively low potential some moments after the start of illumination followed by a slower rise to a stationary value.

We want to discuss the influence of carbon dioxide in a later section. In the mean time it may be remarked here that carbon dioxide has no influence upon the DP as may be seen from fig. 6.

The fact that in the experiment illustrated in fig. 6 the potentials in the presence of carbon dioxide do not tend to return to the original dark level after the light is turned off, is again due to the production of oxygen during the illumination period. This gas was not removed in this particular experiment. The phenomenon was already discussed in section *a* (see fig. 2).

c. *Influence of the anaerobic dark period*

As has been mentioned in the previous section the length of the anaerobic dark period preceding the illumination in carbon dioxide-free media influences the potential behaviour in the light. We have been forced to make use of relatively extended periods of exposure to conditions of low oxygen pressure, as it takes a certain minimum time to expell the air from our suspensions and to allow the electrodes to attain a steady potential. An hour was usually required for this purpose, counting from the start of the introduction of pure nitrogen into the suspension in the manometer vessels. In fig. 7 we have illustrated the result of an experiment in which the anaerobic dark periods have been increased from 72 to 190 minutes. Though the general shape of the curves is similar it appears that both the initial peak and the stationary light level increase with increasing time of anaerobiosis. The reason for this effect is unknown. This makes it, however, difficult to compare different experiments if the anaerobic dark periods are not known accurately.

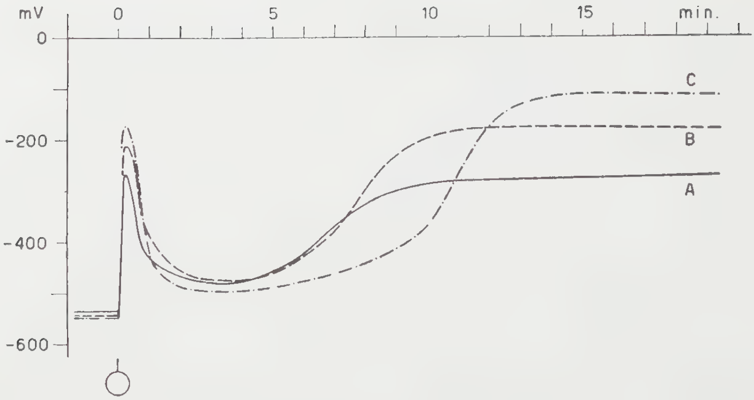


Fig. 7. Influence of the anaerobic dark period.
A: dark period 72 min. B: dark period 100 min.
C: dark period 190 min.

Even so we have found that the response to anaerobiosis varies from one batch to the next as do other details of the potential behaviour such as the depth and length of the low-potential "trough" which was for instance very long in the experiment of fig. 7 but may be quite short in other cases. In general there is a considerable divergency in the properties of different batches of algae notwithstanding the fact that we have standardised the cultivation of the algae as much as possible. It is clear that small differences in the pretreatment of the material may have important influences upon the behaviour during illumination. We have made a point of always measuring the photosynthetic activity of our experimental material simultaneous with our potential measurements in a separate vessel in carbonate-bicarbonate buffer. This has put the fact beyond doubt that minor variations in photosynthetic activity of the algae may be accompanied by important quantitative differences in potential behaviour.

d. The reducing action of intact and disintegrated Chlorella cells

From the foregoing discussions it has become clear that during a certain phase, *Chlorella* cells illuminated in the absence of carbon dioxide may develop the ability to exert a reducing action as evidenced by the oxidation-reduction potential of the liquid surrounding the cells. On the other hand the level of reduction reached during illumination never significantly surpasses the most reduced state reached anaerobically in the dark under favourable conditions. So far, evidence is therefore still lacking that during illumination the cell is developing a more powerful reducing action than in the dark. This is a consequence of the fact that a measurement of stationary oxidation-reduction potentials provides an indication of the degree of reduction of certain constituents of the cell but does not give any information as to the capacity of such systems and some sort of kinetic analysis is needed to settle this point.

The following experiments have led to a decision in this matter. If methylene blue is added to an anaerobic suspension of *Chlorella* at pH 7, the normal DP is not reached within a reasonable time.

If a concentration of methylene blue of between 10^{-5} to 10^{-6} g/L is added, a DP is usually observed of around —230 mV against sat. cal. This value is rather close to the normal redox potential of the dye (about —239 mV on our scale) i.e. in the region where the dye exerts its maximum poising capacity. After very long times of observation or sometimes with particularly active algae the potential ultimately may begin to fall again and in this case the usual DP is finally reached also. This series of events indicates that compared with the amount of dye added the reducing systems of the anaerobic dark processes are of a low capacity. If we now start the illumination before the true dark potential is reached, that is, as long as the methylene blue is still only partly reduced we may observe that illumination results in a quick fall of the potential after which the potential course is the same as in a suspension without methylene blue (fig. 8). As there are indications that illumination in the presence of methylene blue is not a completely harmless treatment to the algae, we have conducted the experiment at a lower temperature (16° C). In fig. 8 this experiment is compared with a blank at the usual temperature of 25° C. This result indicates that at the start of the illumination the methylene blue is much more quickly reduced than in the dark and that therefore the potential determining systems operative during illumination have a larger capacity than those active in the dark. There are indications that small concentrations of oxygen may also be reduced quickly in the induction phase of illumination. We have no very satisfactory evidence at hand, however. Curve *b* of fig. 3 could be interpreted in this way if we extrapolate the potential course after the addition of oxygen in the dark to the point where the induction curve in the light has reached its minimum.

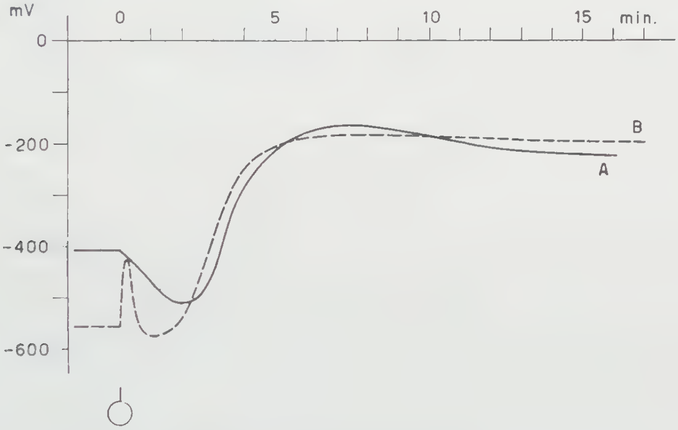


Fig. 8. Reduction of methylene blue during the induction period in the absence of carbon dioxide. A, with methylene blue, temp. 16° C. B, without methylene blue, temp. 25° C. Center vessel with alkaline pyrogallol.

It then appears as if this minimum is lower than the extrapolated dark level. More experimental material would be required to settle this point definitely.

In our opinion the conclusion arrived at above is an important one in relation to an interpretation of the causes of the potential changes during illumination of algal suspensions. It strongly supports the opinion that these potential changes form a reflection of the formation and transformation of reducing substances formed by the photosynthetic system. In this light, the absolute potential values observed may also have some significance. It is perhaps not a mere coincidence that the lowest potential reached during illumination, namely say —560 mV at pH 7.0, is close to the normal potential of the pyridine nucleotides reported recently by BURTON (19). This author has estimated the E^1_0 at pH 7.0 of diphosphopyridine nucleotide to be —320 mV (hydrogen scale) that is equivalent to about —570 mV on our scale (sat. cal.). We might attempt to interprete a curve like *C* of fig. 5 in such a way that about one minute after the start of illumination the pyridine nucleotides in the cells became about half-way reduced. This interpretation gains additional significance in the light of recent experiments whereby it was shown that isolated chloroplasts may reduce pyridine nucleotides (7) and it has been suggested that this reaction may be involved in the photosynthetic carbon dioxide reduction.

In a few experiments with *Scenedesmus quadricauda* at pH 7 a DP of —540 mV was observed. The potential changes during illumination, both in the presence and absence of carbon dioxide, were found very similar to those of *Chlorella.*

Above pH 6 the DP is about the same as the lowest potential reached in the light. One is inclined to assume that in both cases the same reduced compounds are involved. This leads to the following generalised picture. The reductive processes occurring anaerobically in the dark and those induced by the action of the light both lead to the reduction of the pyridine nucleotides. As the two kinds of reductive processes have a limited though different capacity and as dehydrogenative processes may be going on simultaneously, the comparatively large reservoir of pyridine nucleotides in the cell may be considered an effective buffer keeping the oxidation-reduction potential relatively constant notwithstanding important variations in the total amounts of reducing substances present under the different conditions. This region of "buffered" potentials should of course be in an interval of a few tens of millivolts above and below the normal potential of the buffering compound involved.

It is difficult to resist the temptation to speculate a bit further. During photosynthesis the reduced pyridine nucleotides could be used up by two processes. On the one hand they might serve as the sources of reducing power for the reduction of carbon dioxide. On the other hand their removal by simultaneously occurring oxidative processes might furnish the energy for the completion of this carbon dioxide reduction cycle (20). Ultimately the energy is then derived from the photochemical process through the reduction of the pyridine nucleotides. The occurrence of a high concentration of reduced pyridine nucleotides during anaerobiosis in the dark is an indication of their formation also under normal conditions of respiration. They are then continuously removed through oxidative processes so that they cannot reach the same steady-state concentration as in the absence of respiratory processes. Nevertheless their continuous oxidative removal likewise produces a continuous source of the same sort of chemical energy as formed in photosynthesis and they may also be active in similar, though not necessarily identical processes of carbon dioxide reduction. As in this case the energy required for carbon dioxide reduction ultimately is derived from the respiratory consumption of cellular constituents there is no nett uptake of carbon dioxide as is quite obvious.

We have supplemented the experiments reported in this section, with some observations with disintegrated *Chlorella* cells. Though as far as we are aware no method has as yet been described for the isolation of chloroplasts from algae, the method of preparing colloidal extracts from photosynthetic organisms by grinding with carborundum powder (KATZ *et al.* 21) should lead to preparations comparable in many respects to disintegrated chloroplast suspensions of higher plants.

Such disintegrated *Chlorella* preparations, prepared at 2° C and suspended in phosphate buffer, show a pronounced change in oxidation-reduction potential upon illumination (fig. 9). The potential reached anaerobically in the dark is not quite as low as with whole cells but may in favourable cases approach this value. Unlike in suspensions of intact cells the illumination provokes a potential change in the positive direction (curve *B*). As the light is turned off the potential falls again and this series of events can be repeated

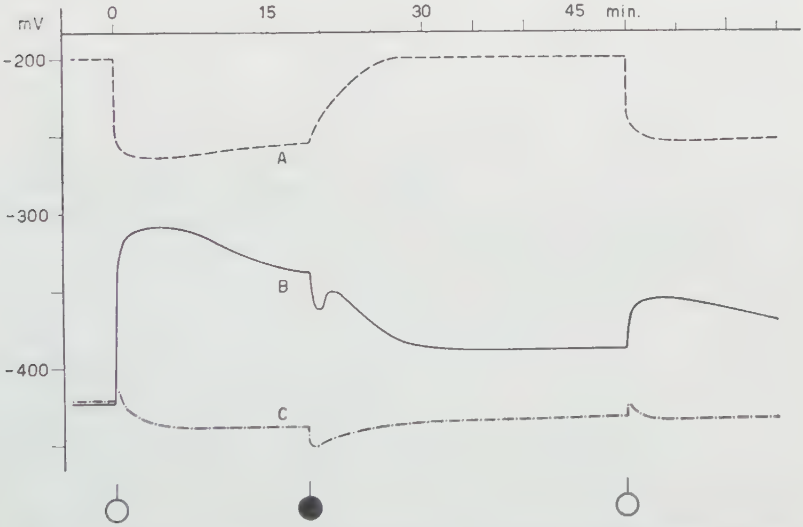
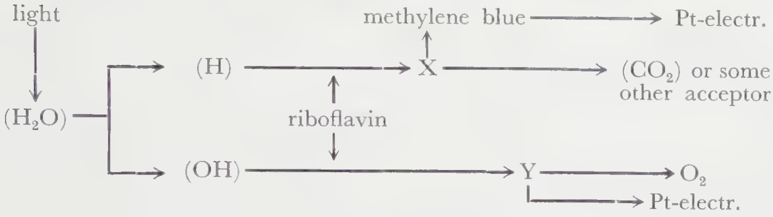


Fig. 9. Potential changes in suspensions of disintegrated *Chlorella* cells.
A: with addition of 1: 10^6 methylene blue. B : no addition.
C: with addition of 1: 10^6 riboflavin.

a number of times though the changes tend to become gradually smaller. This is probably due to an inactivation of the material. That these preparations nevertheless may unfold reductive powers during illumination becomes evident if a small amount of methylene blue (10^{-6} g/ml) is added (curve *A*). This effectively keeps the potential high in the dark, and a comparison with the experiments with whole *Chlorella* cells demonstrates that disintegration has considerably reduced the reductive capacity of the material. However, illumination in this case leads to a quick fall in potential to a level indicating a considerable degree of reduction of the methylene blue. These changes too are reversible upon interruption of the illumination. The addition of a small amount of riboflavin (10^{-6} g/ml) has no influence upon the DP. This is a consequence of the fact that the normal reduction potential of this compound (—220 mV at pH 7.0, i.e. about —470 mV on our scale) is somewhat below the DP. However, upon illumination the presence of this compound effectively suppresses any potential change except for some slight changes at the start and at the end of illumination (curve *C*). It should be added here that addition of riboflavin has no measurable influence upon the potential behaviour of intact *Chlorella* cells.

We would like to offer the following tentative explanation for the reported effects. If we base our discussion upon the simplified assumption that the primary effect of the absorption of light is the splitting of a molecule of water (10), it follows that this primary photochemical act produces equivalent amounts of relatively oxidised and relatively reduced products. From this point of view, no nett change in oxidation-reduction potential should be observable outside the cell under any condition. Ultimately, the relatively reduced compounds lead to the reduction of carbon dioxide and thereby to the formation of non-electrode active compounds. In green cells the relatively oxidised compounds formed, ultimately give rise to the production of molecular oxygen which on a molar basis is only weakly oxidising. Obviously the cell must have an effective means of preventing or at least regulating, the direct recombination of the primary products of the photolysis of water. At any rate, it is more or less a coindence that during certain phases of the illumination period the occurrence of reducing compounds can be directly demonstrated. In disintegrated cell preparations where the normal cellular structure has been destroyed quite other conditions may prevail. We are inclined to conclude that in such disintegrated preparations there is a mixture of various redox-compounds which may be able to react with different speed with the intermediates of the reactions of the photolysis products of water. Depending upon the relative speed with which certain compounds are either hydrogenated or dehydrogenated, an oxidising or a reducing effect may be "transmitted" to the platinum electrode.



Under normal conditions obviously a link is established in a disintegrated preparation between the electrode and the "oxidised line" (see above diagram). Methylene blue, however, appears to react much more quickly with some intermediate (X) of the "reduced line" and this is reflected in a fall in potential upon illumination. It would be in line with the above explanation to assume that whereas riboflavin quickly reacts with the "reduced line" its dihydro form produced in this way will be able to react very quickly with some intermediate of the "oxidised line" as indicated schematically by the arrows. Riboflavin therefore acts so to speak as a short-cirquit between the "reduced" and the "oxidised line". We believe that this picture is not in disagreement either with the observations or with the theoretical deductions made from the experiments with intact cells.

We have been able to obtain results essentially similar to those reported above, with chloroplast preparations of higher plants but we do not intend to go into details in this paper. In the mean time our observations speak against the opinion, expressed by some authors (9, 5) that only redox-compounds with relatively high oxidation-reduction potentials are suitable as Hill reagents, and that in particular, methylene blue is not or only weakly active. We must emphasise that, unlike the majority of previous authors, we have conducted all our experiments in oxygen-free gasses. Undoubtedly, the failure to recognise the effects of oxygen and the presence of oxidising enzyme systems in their preparations, has been responsible for unwarranted conclusions by several investigators as regards the ability of various compounds to serve as Hill reagents. In particular, the failure to demonstrate directly by means of spectro-photometric techniques the formation of dihydropyridine nucleotides in illuminated chloroplast preparations may be due, according to our observations, by the lack of appreciation for the part played by oxygen.

e. The influence of carbon dioxide upon the potential behaviour

As was explained already, the presence of carbon dioxide (as a gas atmosphere of nitrogen containing about 5 % carbon dioxide) has no measurable effect upon the DP's. Upon illumination its presence manifests itself by a very quick rise of the potential to a level which may be as high as 700–800 mV above the dark potential (fig. 6). Again this potential in the presence of carbon dioxide is only weakly dependent upon the pH although we have insufficient material to give a more accurate estimation of the influence of the pH. It appeared that the concentration of carbon dioxide present under these conditions is much too high to study its effect upon the early stages of the potential curve. Actually, very low concentrations of carbon dioxide already produce marked effects upon the course of the potential in the first minutes of illumination. As it was not so easy to add such small doses of carbon dioxide in an accurate way, we have made use of the production by the algae of some carbon dioxide during the anaerobic dark period. In the first place it was shown that anaerobiosis in the dark in a vessel containing no KOH in the center well, led to differences in the potential behaviour during the following illumination. This could be prevented either by adding KOH to the center well or by constantly flushing the vessels with pure nitrogen during the dark period. This led to curves, exactly identical in both cases and we have taken the fact that a volatile compound is obviously formed which can be absorbed by KOH, as sufficient evidence that the compound was carbon dioxide. Actually the effects can be duplicated by the intentional addition of carbon dioxide. By allowing the vessels to accumulate carbon dioxide as the result of varying periods of anaerobiosis, by closing off from the central nitrogen supply at different times, a series of experiments with increasing amounts of carbon dioxide could easily be performed. In fig. 10 the result of such an experiment is illustrated, the numbers in brackets indicating the time in minutes during which carbon dioxide was allowed to accumulate in the dark. In the same figure the result of an experiment in which the gas phase consisted of nitrogen with 5 % carbon dioxide, that is, with a large excess of carbon dioxide is also given. It is of importance to note that the amount of carbon dioxide, formed during anaerobiosis in the dark is so small

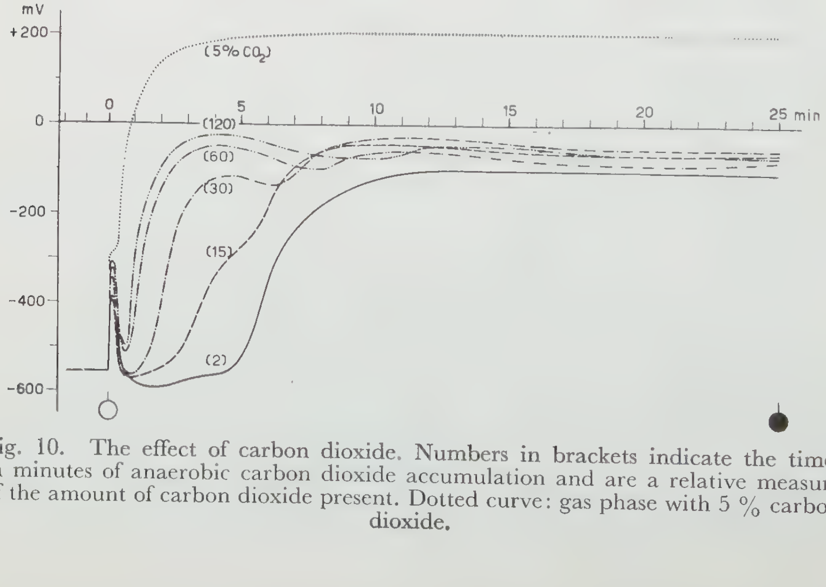


Fig. 10. The effect of carbon dioxide. Numbers in brackets indicate the times in minutes of anaerobic carbon dioxide accumulation and are a relative measure of the amount of carbon dioxide present. Dotted curve: gas phase with 5 % carbon dioxide.

that it is hardly observable manometrically even after two hours. This amount of carbon dioxide is therefore used up quickly during illumination and the righthand parts of the curves in fig. 10 therefore apply to essentially carbon dioxide-free conditions (except of course the upper curve).

From experiments such as the one illustrated in fig. 10 it becomes clear how carbon dioxide influences the potential course during illumination. If we first look at the curve marked (2), i.e. the one applying to an experiment in which carbon dioxide was accumulated during 2 minutes only and which therefore contained the smallest quantity of the lot, we see a slight inflection about 3–4 minutes after the start of the illumination. As the amount of carbon dioxide increases, this inflection grows more and more. The fall, occurring at higher concentrations of carbon dioxide after about 5 min. illumination undoubtedly is associated with the exhaustion of the carbon dioxide. Taking into account this fact, we see that there is a gradual transition to the curve for excess carbon dioxide (top).

The different heights of the peaks immediately after the start of illumination, are due to the fact that in experiments of this kind also the total anaerobic dark period was varied. This in itself leads to an increase in peak height as has been discussed in section *c*. This difference in peak height therefore has nothing to do with the presence of carbon dioxide. We may therefore conclude that the influence of carbon dioxide upon the potential changes in the light is not present immediately after the start of illumination but only sets in gradually and reaches its maximum after about 4 minutes (in this particular experiment!). It is important to note that in several cases we have observed a slight inflection in the potential curve for nitrogen plus 5 % carbon dioxide, about 20–30 sec. after the start of illumination, as illustrated also in fig. 10. This should correspond to the transition from the initial peak to the "carbon dioxide peak" just described. Though it is difficult to measure this inflection accurately owing to its short duration, its demonstration nevertheless is of significance. The consequences of the delayed action of carbon dioxide are important and will be discussed in the next section. We may confine ourselves here to the statement that the effect of carbon dioxide is not immediately observed during illumination, notwithstanding the fact that the carbon dioxide was already present for a considerable time before the start of illumination.

f. The problem of the so-called "persistence of reducing power"

In our opinion, the observations reported in the preceding section form a strong support for the theory that the reducing action of the illumination such as was evidenced already by other experiments (section *d*) is also involved in the mechanisms of the photochemical reduction of carbon dioxide in so far as carbon dioxide removes this reducing material.

Our experiments, therefore, may also throw some light upon the problem of the so-called "persistence of reducing power" formed during preillumination in the absence of carbon dioxide. There has been an important controversy on this question between CALVIN and his collaborators on the one hand and GAFFRON and his co-workers on the other hand (22, 23, 24, 25). From their experiments with labelled carbon dioxide, CALVIN and BENSON (22) concluded, that illumination in the absence of carbon dioxide leads to the formation of a capacity to fix carbon dioxide during a subsequent dark period. They found that this ability to fix carbon dioxide persisted in the dark for some time, the amount of carbon dioxide taken up declining to about one half during a dark period of 5 minutes. In a later paper (23) they demonstrated that the products formed from carbon dioxide during this type of dark fixation are more similar in nature to the products formed during normal photosynthesis than to those formed from labelled carbon dioxide during respiration. It was therefore concluded by these authors that the illumination in the absence of carbon dioxide leads to the formation of compounds, able to reduce carbon dioxide during subsequent exposure in the dark, in the same way as during photosynthesis.

This view was strongly criticised by GAFFRON *et al.* (24, 25), who maintain that the effect of preillumination is only in removing carbon dioxide from intracellular "carbon dioxide reservoirs" and that subsequent exposure to carbon dioxide in the dark leads to a replenishment of such reservoirs. This point of view received support from the experiments of MEHLER (9) who observed no persistence of the ability to reduce Hill reagents after preillumination of chloroplast preparations.

It would appear that our experiments in principle are able to give a decision between these controversial viewpoints. We have therefore performed the following experiments. *Chlorella* cells were preilluminated for a certain period without carbon dioxide and the potential was observed. At a suitable moment, the light was turned off, and carbonic acid was added to the suspension as quickly as possible.

The method employed was as follows. As preliminary experiments had indicated, introduction of carbon dioxide gas did not guarantee a sufficiently quick addition. We therefore have put into our suspensions small thin-walled glas bulbs completely filled with an oxygen-free solution of sodium bicarbonate. The bulbs could be broken without opening the vessels or interrupting the shaking (see experimental part). In this way it was possible to add the carbonic acid within half a second after the light was turned off and the first potential reading could be taken about ten seconds later.

As a rule, potentials start to return to the dark level immediately after the light is turned off. This process is rather slow however. If there was any persistence of the ability to reduce carbon dioxide, and this ability should persist for periods of minutes, we might expect to see the potential approach the level of a carbon dioxide-containing experiment during the first seconds after the light was turned off and the carbon dioxide added. The curve should then slowly fall to the dark level again. As may be seen from fig. 11, this expectation was not fulfilled under any experimental condition. Experiment 11*a* shows what happens if carbon dioxide is added in the manner described, to a carbon dioxide-free suspension during illumination (open circles). In the same figure is given the course of the potential if the light is simply turned off at the same moment without addition of carbon dioxide (black circles). As was expected, the curve for carbon dioxide rises more quickly than does the curve for the darkened suspension

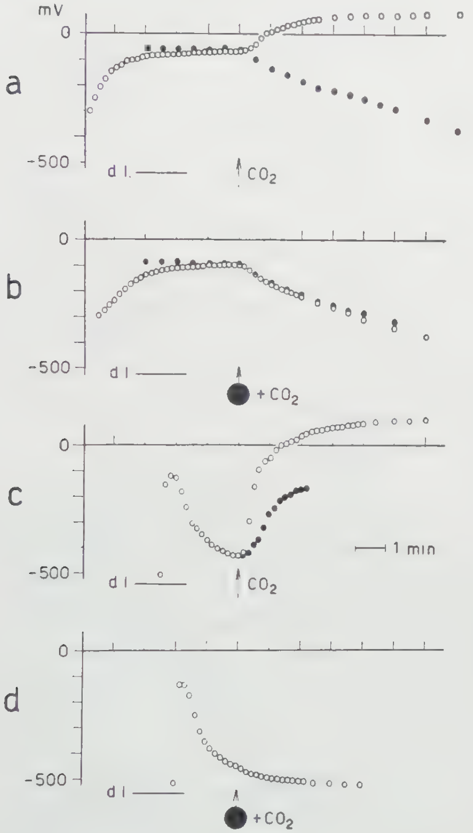


Fig. 11. Addition of carbon dioxide during illumination and after pre-illumination in the absence of carbon dioxide.

a. Stationary phase. Bicarbonate added in the light (○), or light turned off. (●).

b. Stationary phase. Bicarbonate added immediately after light was turned off (○), and no bicarbonate added in the dark (●).

c. Induction phase. Bicarbonate added in the light (○), or no bicarbonate added (●).

d. Induction phase. Bicarbonate added immediately after light was turned off.

fall. In experiment 11*b*, carbon dioxide was added to one vessel immediately after the light was turned off (open circles). It is obvious that the potential follows exactly the same course in the dark as in a suspension to which no carbon dioxide was added (black circles). Both experiment *a* and *b* were done in the stationary state of the potential curve (for the sake of clarity, all parts of the potential curve, not essential to the present experiments, have been omitted. The dark potentials before the illumination was started are indicated by the lines marked d.l.). One could remark, however, that the reducing tendency of the light would become apparent only during the first minutes of the illumination. The experiments described above have been repeated, therefore, during this phase of the potential changes (expt. 11*c* and 11*d*). The results were essentially the same. In experiment 11*c*, the potentials in the light, after carbon dioxide addition (open circles) have been compared with the potentials in the light without such addition (black circles). In experiment 11*d*, the addition of carbon dioxide had been preceded by interruption of the illumination and it is seen that the potential returns to the dark level quickly.

The experiments reported in this section have therefore failed to demonstrate a survival of reducing power following illumination in the absence of carbon dioxide and from this point of view, they are in better agreement with the views expressed by GAFFRON and coworkers than with those of CALVIN and his associates. We believe, however, that our experiments do not support the conclusion that no reducing power survives in the dark but merely that in the dark, carbon dioxide does not react with such reducing compounds, if formed. We want to stress the fact, that such a situation is not at all unexpected. It is now generally accepted that it is not the carbon dioxide itself which enters into the reaction with the reducing agents but that the carbon dioxide is first incorporated into certain intermediates in non-photochemical processes. Such intermediates then may react with the reducing compounds to form products which may be looked upon as representing reduction products of carbon dioxide. Such a scheme supposes the presence in the photosynthesising cell of specific compounds able to react with carbon dioxide to form the intermediates which can be reduced by the products of the photochemical process. We may call such a compound the photosynthetic carbon dioxide acceptor. The experiments of CALVIN (26) and of GAFFRON (25) have indicated that this carbon dioxide acceptor may be a two-carbon compound forming with carbon dioxide phosphoglyceric acid which may react with the reducing compounds from the photochemical process to form phosphoglyceraldehyde, which is then transformed in a reversal of the glycolytic pathway into carbohydrate.

In the following discussion we will base ourselves upon a scheme for the photosynthetic cycle which is a modification of those proposed by other workers. It must be stressed, however, that the precise details of such a process are not important for our present purpose and that this scheme therefore merely serves as an example.

$$\begin{tikzcd}
 & 6\,CO_2 \arrow[d] & & & \\
6\,C_2 \arrow[rr] & {} & 6\,C_3 \arrow[dd] & & {} \arrow[d, "h\nu"] \\
 & & {} & (H) \arrow[l] & (H_2O) \arrow[l] \\
9\,C_2 \arrow[uu] \arrow[d] & & 6\,C_3H_2 \arrow[ll] & & \\
3\,C_2 \arrow[r] & C_6 & & &
\end{tikzcd}$$

In section *e* it was shown that carbon dioxide, even if present from the start, does not consume reducing power in the light until after some moments. Nevertheless, this reducing power is formed immediately upon illumination (e.g. fig. 5*C*, fig. 8.*1*). In our opinion this indicates that at the start of the illumination only a small amount of the carbon dioxide acceptor (C_2) is present, which has to be built up before carbon dioxide reduction can assume a measurable speed. This acceptor is therefore not formed from carbon dioxide in the dark to any appreciable extent.

If carbon dioxide is added to a suspension of algae during illumination, several minutes are required before the potential reaches its maximum steady value (fig. 11*a* and *c*). As it must be supposed that in this case, the reducing systems were already operating, we may draw the following conclusion from this induction period in the effect of carbon dioxide. During illumination in the absence of carbon dioxide the reducing system is present but the concentration of the carbon dioxide acceptor system remains low. As soon as carbon dioxide is added, more acceptor begins to be formed until the final level required for steady state photosynthesis is reached. The addition of carbon dioxide after pre-illumination (fig. 11*b* and *d*) therefore is not followed by a rise in potential as the carbon dioxide is not transformed to a significant extent into a compound which can react with the reducing compounds formed in the light. This picture therefore does not exclude the possibility that reducing compounds survive in the dark. It merely indicates that they cannot be demonstrated because of the lack of suitable carbon dioxide acceptors. The conclusion we may therefore draw from our experiments is that the amount of carbon dioxide acceptor required for steady state photosynthesis cannot be formed unless by the simultaneous and combined action of light and carbon dioxide.

At first sight it might appear that the picture, presented above, does not agree with the results of isotope studies (24). From experiments of such kind, GAFFRON and co-workers have concluded that the carbon dioxide pick-up following preillumination in the absence of carbon dioxide leads mainly to the formation of phosphoglyceric acid, so that under "carbon dioxide-free" illumination the same carbon dioxide acceptor appears to have been formed as during normal photosynthesis. The discrepancy with our experiments probably is only of a quantitative nature. In order that photosynthesis can start at all, at least a small amount of carbon dioxide acceptor has to be present at the start of illumination. The amount of hydrogen acceptor formed from it may be much too small to be demonstrated by our potentiometric methods but the same does not apply to tracer methods. Moreover, as we have shown it is practically impossible to work in the complete absence of carbon dioxide even if respiration is excluded. What we believe to have demonstrated is therefore, that though some carbon dioxide acceptor may be present after a long dark period, the bulk of this substance present during normal photosynthesis is only formed as a result of the action of light and carbon dioxide, that is to say that it is itself a product of photosynthesis. This point of view agrees well with the observation that already after relatively short periods of photosynthesis with labelled carbon dioxide the phosphoglyceric acid formed becomes uniformly labelled (27). We are of the opinion that the picture presented above may throw considerable light upon the induction phenomena associated with the photosynthetic process.

g. Influence of KCN

The influence of KCN upon photosynthesis is variable, some organisms being strongly inhibited, others hardly (28). For *Chlorella* it has been shown that concentrations of 10^{-4} M already are markedly inhibitory to the gas exchange in the presence of carbon dioxide (29). We have studied the influence upon the potential behaviour and have been very surprised to see that this poison is already active in very small concentrations indeed (fig. 12). Concentrations as low as 10^{-6} M are sufficient to suppress the potential changes during illumination almost completely. The effect of KCN is mainly upon the dark potentials, in agreement with the conclusion, arrived at in section *b* viz. that the DP's and LP's are governed by separate processes. It is, however, difficult to give an explanation for the unusually low concentrations in which the poison is active. One possibility is that hydrocyanic acid is poisonous to the platinum electrodes. A direct chemical reaction with the redox-compounds, transmitting the potentials to the electrode is also not to be excluded completely. At the moment we are unable to offer a satisfactory explanation for the effect of KCN.

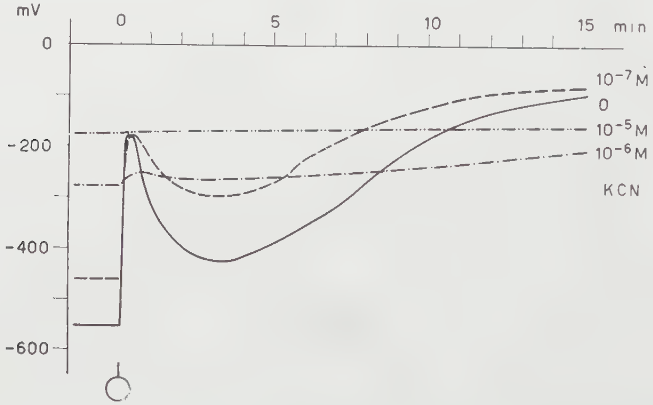


Fig. 12. Effect of potassium cyanide upon the potentials in an experiment without carbon dioxide. Cyanide concentrations in the suspension indicated behind the curves.

We have also studied the influence of KCN in experiments with carbon dioxide. It is difficult under these conditions to keep the hydrocyanic acid in the suspension during the long-continued deaeration with the carbon dioxide containing gas mixture. This has made the estimation of the amounts of HCN present in the suspension a bit uncertain, but there can be no doubt that also in this case the effect upon the potential is very strong and is in the same concentration range as for experiments without carbon dioxide. We have been able to confirm by direct measurement of gas exchange that in this concentration region (10^{-7} — 10^{-5}) there was no significant influence of the HCN upon carbon dioxide assimilation.

h. *Influence of light intensity upon the potentials*

We have measured the changes in oxidation-reduction potential as a function of time during illumination, for a number of intensities of the irradiating light.

In all the experiments discussed so far, the light intensity was approximately the same, viz. about 4 × 10^4 erg/cm² sec. We have obtained the lower intensities by placing glass filters under the manometer vessels. A set of 6 vessels was always employed simultaneously, each containing suspensions of the same batch of algae and receiving a different irradiating intensity. In this way it was possible to obtain from one experiment the potential-time curves at six different intensities. Afterwards sections could be made through the sets of curves so obtained, giving the potentials as a function of light intensity at any desired time from the start of illumination.

In fig. 13 some of the curves so obtained are given, the numbers behind the various curves indicating the times in minutes after the start of illumination. We have chosen for illustration two curves for each experiment, one for a moment during the induction period, the other in the stationary phase of the potential-time curve. The

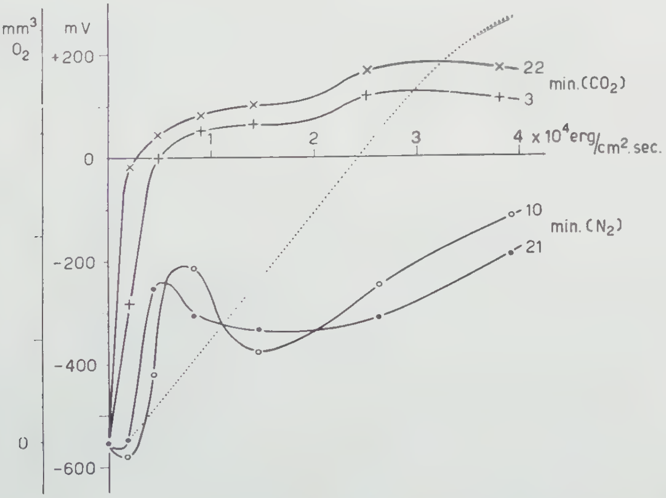


Fig. 13. Potentials as a function of light intensity. Upper two curves with addition of carbon dioxide. Lower two curves without carbon dioxide. Numbers behind curves indicate the times after start of illumination. Dotted curve: photosynthesis. This applies to the experiments with carbon dioxide.

lower two curves represent the results of an experiment with pure nitrogen as the gas phase, the others apply to an experiment with nitrogen plus 5 % carbon dioxide. For the latter experiment, the result of the simultaneous determination of gas exchange is also given in arbitrary units as the dotted line.

This assimilation curve was obtained with the one-vessel method assuming an assimilatory quotient of unity.

We have felt the necessity for carefully checking the results of this type of experiments. As has been explained in the Experimental Part, the platinum electrodes may become unreliable, and a vessel containing such electrodes would lead to wrong conclusions. We have therefore proceeded as follows. After the conclusion of a complete measurement the vessels were put in the dark again. As soon as the potentials had nearly reached the original dark potential the light filters under the vessels were replaced (in the dark) so that each vessel received a different filter than before. The complete experiment was then repeated. Though we have never been able to reproduce exactly the curves found in the first run (this was not expected either, on the basis of our previous experience with repeated illumination) we were satisfied to note that the maxima and minima in the curves fell at approximately the same light intensities and were not, therefore, due to pecularities of a particular set of platinum electrodes. We therefore feel confident that the unusual form of the curves in fig. 13 is real.

An attempt to explain the shape of the potential-intensity curves would appear impossible at the moment. We will only note that as far as we can judge from these experiments, there is no relation with light-saturation of photosynthesis. If we may speak of a light-saturation of the potentials in experiments with carbon dioxide present, this saturation occurs at an intensity at least one tenth of that required for saturation of photosynthesis. Moreover, a comparison with the curves for pure nitrogen shows that the light-intensity region of $0.5 — 1 \times 10^4$ erg is of particular importance in both conditions and that the occurrence of extrema in this region is not, therefore, connected with the presence of carbon dioxide.

In making a comparison between the light intensity functions of gas exchange and potentials, it should be kept in mind that photosynthesis represents a reaction velocity whereas the potentials, especially those measured during stationary conditions, indicate concentration ratios of oxidation-reduction systems and thereby of reducing or oxidising capacities[1].

Finally, the outcome of these experiments bears some relation to the work of other authors. STREHLER *et al.* (30 and 31) have reported experiments on the luminescence of chloroplasts and intact *Chlorella* cells, following irradiation. They have also measured potentials in such systems, assuming them to give a measure of the rate of the Hill reaction. In the first place we believe that our experiments have shown that the last-mentioned conclusion is very dangerous. Further, these authors have measured the potentials in such systems as a function of light intensity and have shown that luminescence and potentials follow almost the same course. The results discussed in this section clearly demonstrate that the light

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[1] The author is indebted to Prof. Dr E. C. WASSINK for this remark.

"saturation" observed by *Strehler*, is no real saturation and is not related to light saturation of photosynthesis. It is nevertheless very interesting to compare the figure 3 on page 811 of their publication (30), which gives the luminescence of *Chlorella* as a function of the exciting light intensity, with our figure 13. They are of exactly the same nature and it is tempting to suggest that the luminescence phenomena observed by these authors are related to the oxidation-reduction reactions we have discussed in the present paper.

IV. CONCLUDING REMARKS

Many of the conclusions, arrived at in this paper have a preliminary nature. We believe to have shown beyond doubt, however, that the changes in oxidation-reduction potentials measured in suspensions of *Chlorella* are connected in some way or other with processes, particular to the mechanisms of photosynthetic carbon dioxide reduction. They are not, however, connected directly with the effects of over-all photosynthesis, an observation already reported earlier by WASSINK for experiments with purple bacteria (13, 32). In addition, our experiments strongly support the idea that, at least during certain phases of the induction period the potentials are a reflection of the formation of reducing compounds by the primary photochemical process which are suitable as hydrogen donors for carbon dioxide reduction.

Finally we want to direct attention to the fact that the induction phenomena reported here bear a great deal of resemblance to induction phenomena of other aspects of photosynthesis. This does not so much apply to the induction of total gas exchange but more to phenomena such as chlorophyll fluorescence (WASSINK, 33, 34) and phosphate metabolism (KANDLER 35). We hope to be able to study the relations between these various phenomena in some detail later.

SUMMARY

A study has been made of the oxidation-reduction potentials in suspensions of algae. The potential was found to be governed by three systems, viz. *1*, the respiratory system, *2*, a metabolic process occurring in the dark in the absence of oxygen, and *3*, a system connected with the photosynthetic processes, exclusively determining the potential changes in the light below a certain oxygen tension. The activities of these systems may be distinguished on the basis of their different sensitivities to oxygen, pH and enzyme poisons.

At the start of illumination the potential shows a pronounced induction phenomenon and a stationary potential is reached after about 15 min. illumination. Oxygen and hydrogen peroxide are not involved in the establishment of this stationary potential.

The essential feature of the potential behaviour in the light and in the absence of carbon dioxide irrespective of pH is that a relatively reduced state is reached some minutes after the start of illumination.

Afterwards the potential rises again slowly to its stationary value. During the initial phase of low potentials, methylene blue and possibly also oxygen may be reduced by the suspensions. Similar experiments with disintegrated *Chlorella* cells demonstrated that both oxidising and reducing reactions occur.

The presence of carbon dioxide during illumination results in a more positive potential. This can be explained by assuming that the reducing compounds formed by the action of light are removed by reaction with carbon dioxide. The action is exerted by extremely small concentrations of carbon dioxide. Its maximum effect occurs about 1–2 min. after the start of illumination.

No persistence of the ability to reduce carbon dioxide in the dark after preillumination in the absence of carbon dioxide was observed.

Our observations lead to the hypothesis that in the dark a very low concentration of the photosynthetic carbon dioxide acceptor is present. The establishment of steady state photosynthesis involves the formation of a sufficient amount of this carbon dioxide acceptor under the simultaneous and combined action of light and carbon dioxide.

The potentials depend upon the light intensity in an unusual way. There is no relation to the light saturation of photosynthesis.

The author is indebted to Prof. Dr E. C. Wassink for the stimulation to start this investigation and for valuable discussions, to Mr M. F. Kerkhof Mogot for experimental assistance and to Mr H. van den Brink for the construction of the manometer vessels.

REFERENCES

1. Hill, R. and R. Scarisbrick, Nature *146*, 61 (1940).
2. Warburg, O. und W. Lüttgens, Naturwiss. *32*, 161 (1944).
3. Aronoff, S., Plant Physiol. *21*, 393 (1946).
4. Holt, A. S., R. F. Smith and C. S. French, Plant Physiol. *26*, 164 (1951).
5. Wessels, J. S. C. and E. Havinga, Rec. Trav. Chim. *71*, 809 (1952).
6. Fan, C. S., J. F. Stauffer and W. W. Umbreit, J. Gen. Physiol. *27*, 15 (1943).
7. Vishniac, W. and S. Ochoa, J. Biol. Chem. *195*, 75 (1952).
8. Tolmach, L. J., Arch. Biochem. Bioph. *33*, 120 (1951).
9. Mehler, A. H., Arch. Biochem. Bioph. *33*, 65 (1951).
10. Niel, C. B. van, Arch. Mikrobiologie *3*, 1 (1931).
11. Spikes, J. D., R. Lumry, H. Eyring and R. E. Wayrynen. Arch. Biochem. Bioph. *28*, 48 (1950).
12. Tang, P. S. and C. Y. Lin, J. Cell. Comp. Physiol. *9*, 149 (1937).
13. Wassink, E. C., Antonie van Leeuwenhoek *12*, 281 (1947).
14. Wassink, E. C., Rep. Proc. 4th Int. Congr. Microbiol. p. 455.
15. Kluyver, A. J. and J. C. Hoogerheide, Enzymologia *1*, 1 (1936).
16. Warburg, O. Bioch. Z. *100*, 230 (1919).
17. Veen, R. van der, Physiol. Plantarum *3*, 247 (1950).
18. Clark, W. M. and B. Cohen, Hygienic Laboratory Bulletin, U.S. Public Health Service, *38*, 666 (1923).
19. Burton, K., Bioch. Bioph. Acta *8*, 114 (1952).
20. Kok, B., Enzymologia *13*, 1 (1948).
21. Katz, E. and E. C. Wassink, Enzymologia *7*, 97 (1939).
22. Calvin, M. and A. A. Benson, Science *107*, 476 (1948).
23. Benson, A. A. and M. Calvin, J. Exp. Bot. *1*, 63 (1950).

24. FAGER, E. W., J. L. ROSENBERG and H. GAFFRON, Federation Proc. *9*, 535 (1950).
25. GAFFRON, H., Symp. Soc. Exp. Biol. *5*, 262 (1951).
26. CALVIN, M., J. Chem. Education *26*, 639 (1949).
27. CALVIN, M., J. A. BASSHAM and A. A. BENSON, Federation Proc. *9*, 524 (1950).
28. RABINOWITCH, E. I., Photosynthesis, vol. I (1945).
29. WASSINK, E. C., D. VERMEULEN, G. H. REMAN and E. KATZ, Enzymologia *5*, 100 (1938).
30. STREHLER, B. L. and W. ARNOLD, J. Gen. Physiol. *34*, 809 (1952).
31. STREHLER, B. L., Arch. Biochem. Bioph. *34*, 239 (1951).
32. WASSINK, E. C., Symp. Soc. Exp. Biol. *5*, 251 (1951).
33. WASSINK, E. C. and E. KATZ, Enzymologia *6*, 145 (1939).
34. WASSINK, E. C., Advances in Enzymology *11*, 91 (1951).
35. KANDLER, O., Z. Naturforschung *5b*, 423 (1950).

A RE-EXAMINATION OF CESALPINO'S CLASSIFICATION

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In all works dealing with the history of botany a more or less important place is allocated to Cesalpino's "De Plantis Libri XVI", (1583). This is easily comprehensible for even a cursory inspection of this book can not fail to impress us with the author's originality and his unusual gifts for analysis and exposition. The most important part of the work, viz. the books II–XVI, is devoted to a survey of the plants that were known at that time, and contains an attempt to arrive in a truly scientific way at a classification of the latter, and if the reader is acquainted with the earlier works in which a survey of the plant world is given, he will realize that Cesalpino was the first to make such an attempt. It is, however, not only the novelty of the enterprise that excites our admiration, but also the acumen with which it is carried into effect. Unfortunately, but few botanists seem to have read the book, and even the majority of the authors on the history of botany apparently did not deem this necessary. At least, most of them based their conclusions on the abstract given by Linné in his "Classes Plantarum", and this abstract is, as I will show hereafter, very incomplete and in some respects even incorrect. A laudable exception to this rule is found in the essay on Morison and Ray that Vines contributed to Oliver's "Makers of British Botany"; Vines' survey of Cesalpino's system differs but in minor points from the one given below.

In Sachs' "Geschichte der Botanik", of which an English edition appeared under the title "History of Botany", an analysis of Cesalpino's work is found that deserves our special attention. It is true that Sachs' conclusions with regard to Cesalpino's classification are based on the abstract given by Linné and are therefore untrustworthy, but his exposition differs from that of all earlier authors in the thoroughness with which he discusses the contents of the last three chapters of Book I, in which Cesalpino expounds the principles on which his classification is based, and in which he tries to justify their choice. It appears that Sachs was fully aware of the truly scientific spirit with which these chapters are imbued, and by which they tower high above all that ever before had been written on this subject. In fact, Cesalpino was in this respect so far ahead of his time that for the next hundred years nobody seems to have understood him. SACHS certainly displayed a great admiration for CESALPINO's genius, but he was nevertheless not sufficiently impartial to do him full justice. The reason for this somewhat contradictory attitude is to be sought in his aversion for CESALPINO's philosophical standpoint.

CESALPINO was not only a gifted botanist, but he was also a philosopher who occupied himself with the Aristotelean doctrine. In fact, he was so well versed in the latter that he wrote a book on it, which was published under the title "De questionibus peripateticis". He showed himself in this work an adherent of the neo-scholastic school which at that time in the towns of northern Italy played a leading part in intellectual circles, and differed from the older scholastic schools by concentrating its attention especially on those works of ARISTOTLE that deal with the science of nature. However, it was, like its predecessors, inclined to place a too implicit faith in the words of the master, and it was mainly against this tendency that SACHS felt himself bound to do battle. This, of course, was his good right, but in his rationalistic zeal he sometimes overshot the mark. It certainly can not be denied that CESALPINO derived part of his ideas from ARISTOTLE, and it is not difficult to show that some of them were unfounded assumptions that led him astray, but in general the influence of ARISTOTLE on CESALPINO was by no means so disastrous as SACHS' exposition is apt to suggest. On the whole it is the form in which CESALPINO presents the results of his studies that reminds us of the Stagirite, and although this form may sometimes be objectionable, it should not blind us for the significance of the results themselves. Most of us will agree that in judging the scientific value of works written in the past we must leave the author's philosophical or theological orientation as much as possible out of consideration, as this value is, as a rule, but slightly influenced by these factors. When we place ourselves on this standpoint, the unusual vigour of SACHS' attack will strike us as out of all proportion to CESALPINO's offences.

The point against which SACHS' attack mainly is directed, is CESALPINO's use of the term "cor" or "heart" and his valuation of the functional importance that the part to which this term is applied, should possess. The part indicated as "cor" is the transition zone between the root and the shoot. This zone does not exactly correspond to the part that we nowadays know as the rootneck, for according to CESALPINO it extends upwards to the place where the cotyledons are inserted, which means that it includes the hypocotyl. From the fact that at this place in the undifferentiated embryo the separation between root and shoot is effected, CESALPINO somewhat hastily concludes that it must be the seat of an agency that directs the root downwards and the shoot upwards. To us it looks unlikely that this but vaguely differentiated zone, which moreover is absent in plants grown from cuttings, should be able to exercise a directing function, and we now know that in the shoot as well as in the root the direction of growth is not determined at this place but in the parts themselves, viz. in their growing zones. However, we should not forget that the way in which in the embryo the separation between root and shoot is effected, remains to this day an unsolved riddle, and we should credit Cesalpino at least for having recognized that this separation presents a problem. Moreover, we should realize that Cesalpino's solution, although unacceptable to us, will have sounded plausible enough at a time when those who occupied themselves with biological problems, were inclined to draw a very close parallel between plants and animals, and who therefore, as the existence of such a directing influence in the centre of the animal body was generally accepted, could have no objection against the assumption of a similar directing agency in the centre of the plant body. As in the animal body this function was in Cesalpino's time thought to be performed by the heart, it was only natural that he transferred this name to the part of the plant body that in his opinion fulfilled a similar office.

Further on we will discuss Cesalpino's opinion that the characters on which the classification is to be based, should be derived from the number, position and general aspect ("numerus", "situs", "figura") of functionally important parts. For the moment it suffices to realize that from his point of view the transition zone between root and shoot certainly belonged to these parts, and that he will therefore have felt himself fully justified in using the position of this part in the seed, and eventually in the fruit, for the subdivision of some of his groups. However, he used it but sparingly, and the impression created by Sachs' exposition that it was one of the main principles of his classification is certainly wrong. In discussing the two main divisions of the woody plants he points out that in the first the seeds are attached in such a way to the pericarp that the "heart" is turned towards the outside ("semina eo modo sedent ut cor exterius vergat"), whereas in the second the seeds are inserted in such a way that the "heart" is turned towards the point of insertion ("semina eo modo sedent ut cor ad sedem vergat"), but he is well aware of the fact that this is no rule without exception, and the division is not based on this difference but on the number of seeds per fruit. Among the herbaceous plants he twice mentions a pair of groups that are said to differ in this way. They are discussed in book IV and in book XI, and in the summary given at the end of this paper they are numbered respectively 14 and 15, and 27 and 28. In group 14, which comprises the *Chenopodiaceae*, *Urticaceae* and *Cannabinaceae*, the rootlet is described as turned upwards ("seminis cor exterius"), and in group 15, the *Gramineae*, as turned downwards ("seminis cor inferius"). Of group 27, which comprises the *Boraginaceae*, it is said that the rootlet is found at the top of the "seed" ("cor in summo"), whereas in group 28, the *Labiatae*, the rootlet is said to be at its base ("in sede vim genitalem gerunt"); with "seed" in both families the nucule is meant, and "vis genitalis" is another term for "cor": it indicates the power of the rootlet to break through the testa. Cesalpino's words are quoted here in detail in order to make it clear that the position of the embryo plays but a subordinate part in his classification, and that Sachs therefore attached too much weight to this point. It is perhaps not superfluous to add that the subsequent development of our knowledge in the field of Angiospermous morphology has shown that the position of the embryo in the seed, which proved to be correlated 1° with the structure of the ovule (atropous or anatropous) and 2° with the latter's position (ascending or descending), is in reality a much more valuable character than CESALPINO could have presumed, and it put SACHS entirely in the wrong. CESALPINO deserves adequate recognition for having been the first to draw the attention to this character.

CESALPINO's view that the characters on which the classification is to be based, should be taken from those parts that play an important part in the life of the organism, returns in the works of most of his successors. In fact, it maintained itself until it was superseded by the Darwinian view that these characters should on the contrary be taken from parts that are functionally of little or no importance. The adherents of the Darwinian variant of the evolution theory argued that the characters of functionally important parts are too much subject to the influence of natural selection to become stabilized, and that their taxonomic importance therefore can not be very great. It is easy to see that this dogmatic view does not agree with observed facts, for although it can not be denied that there are numerous characters of taxonomic importance of which we can hardly expect that they should prove of any value in the life of the organism, e.g. such characters as are presented by the relief of the pollen grains, there are also taxonomically important characters that are of the utmost functional importance, e.g. the colour of the chromatophores in the different groups of *Algae*, which determines the depth beneath the surface at which these organisms can live.

CESALPINO was probably well aware of the fact that the characters on which he based his divisions, were themselves on the whole of little or no importance to the life of the plants. At least he says nowhere that they are, but confines himself to the statement that they are taken from parts of functional importance. The same phrase is met with in the works of LINNÉ. It seems hardly probable that the latter would not have seen that the characters on which he based his sexual system, viz. the number of the stamens and carpels, their freedom or coalescence, etc., could hardly be of importance in the life of the plants, and the reproof that he received on this account, e.g. from SACHS, is in my opinion unfounded. It must, on the other hand, be admitted that the phrase "derived from parts that are functionally important" has very little meaning. The functions that according to CESALPINO are of importance in the life of the plant, are nutrition and reproduction, and as all parts of the plant are in one way or another involved in one of these functions, it seems impossible to find a character that is not taken from such a part.

The explanation of this at first sight rather puzzling attitude is indeed to be found in an exaggerated respect for the views of ARISTOTLE. As the latter had mainly confined his classificatory interest to animals, it is not very amazing that he saw no difference between taxonomic and functional importance. Fishes are characterized by their adaptations to the life under water, birds by their ability to fly, mammals by the way in which they feed their young, the various groups of mammals by the adaptations shown by the organs with which they obtain their food and by those of the teeth with which they work on it, etc. However, as soon as this principle was applied to plants, it led to difficulties, as indeed it also does when more rigorously applied to the animal world. This is what Cesalpino, and afterwards Linné, experienced, and it was in order to save the Aristotelean principle that they made the concession mentioned above: although the characters themselves need not play an important part in the life of the plant, the parts from which they are taken, should fulfill this condition. The concession, of course, does not really save the principle, for the functional importance of a part evidently rests on the functional importance of some of its characters, and if the principle was a sound one, those characters that are responsible for the functional importance of the part, should be chosen, not the indifferent ones. However, in judging the trials and errors of these pioneers in the domain of taxonomy, we should not forget that the need for such a "logical" justification was felt very strongly in their time, and that without this addition, which to us is hardly more than a literary embellishment of somewhat doubtful taste, their systems would not have been acceptable to their contemporaries.

The artificial nature of the arguments by means of which Cesalpino tried to make the choice of his characters acceptable, makes it probable that these characters were not, as it is customary to assume, chosen on account of a preconceived notion, but that they must have been brought to light by the analysis of natural groups, i.e. of groups of plants that are similar in habit. In this respect, at least, the method of the earlier taxonomists will not have differed from that of their modern colleagues. Their procedure, however, will have deviated from that of the later taxonomists herein that they will have started with a very small number of natural groups, perhaps with a single one, their experience in this field being insufficient to recognize at first sight more than a very few of them. They will have completed their classification by the establishment of groups based on characters of a kind that had been found serviceable for diagnosing the original groups. Experience has taught us that this does not necessarily lead to satisfactory results, and that this kind of classifications always contain a number of more or less heterogeneous groups. Another reason for the heterogeneity of the groups of the earlier taxonomists lies in the circumstance that the parts from which the characters were taken, were not always homologous. Cesalpino mistook small one-seeded fruits for seeds, and this explains why we find *Ficus* and *Opuntia* next to each other in the same group, and the *Ranunculaceae* and *Compositae* are placed in each other's vicinity because he saw no difference between fruits that develop inside a single flower and fruits that owe their origin to a flower-like inflorescence.

The best way to obtain an idea of the manner in which CESALPINO will have proceeded, will be that we attempt to reconstruct it. As stated above, it is impossible for us to assume that he arrived at his classification in the way expounded in the concluding chapters of book I. The arguments which according to this exposition lead to the choice of his characters, were merely arguments by which he tried to justify the choice after the latter had been made, and by which any other choice could have been justified as well. This is a curious logical flaw, for which, however, we should not blame CESALPINO too much, seeing that the phylogeneticists of our own time commit the same offence. They too place the theoretical interpretation of their systems, which are arrived at in exactly the same way as those of non-phylogeneticists, in front, and speak of a "phylogenetic method"!

CESALPINO's starting point will have been one of the strikingly uniform groups such as the *Umbelliferae*, the herbaceous *Leguminosae*, the *Liliiflorae* or the *Compositae*. Let us suppose that he started with the *Liliiflorae*, i.e. with group 26 of the list given below. He will have noted that the representatives of this group are herbaceous plants provided with 3–locular fruits and with swollen underground parts. As a division of the herbaceous plants, the group he accepted from his predecessors and whose naturalness he did not doubt, on account of the nature of the underground parts could not appeal to him, he will have turned his attention to the structure of the fruit. His next step therefore will have been the examination of the remaining herbs with 3–locular fruits. He will have seen that these plants do not form a natural group, but that some of them nevertheless are very similar, and as the latter proved to possess a single seed in each cell, he will have divided these plants in two groups, one with one-seeded fruit cells and the other with several seeds in each cell. Therefore, as the presence of 3–locular fruits proved a useful character for diagnosing these three groups, he will have turned his attention towards plants that correspond with each other by the presence of another number of fruit cells. In this way he will have detected that the plants with 2–locular and those with 4–locular fruits form fairly uniform groups, and he will have noted that in the case of the plants with 2–locular fruits an even more natural arrangement could be obtained by dividing them according to the same set of characters that had proved useful for the subdivision of the plants with 3–locular fruits, viz. the presence of one or more than one seed in each fruit cell. This subdivision led in the plants with 2–locular fruits to the splitting off of such well-defined groups as the *Umbelliferae* and the *Cruciferae*. This success will have encouraged him to proceed in the same way.

Instead of starting with the *Liliiflorae* he may have begun with another natural group, e.g. the *Umbelliferae* or the *Compositae*, but as the final result would have been the same, this is a point of minor importance. However, it is also possible that he started with a comparison of two or three of the natural groups, but it seems more probable to me that he followed the first course, because that would have led him to the discovery of a larger number of natural groups, and this, of course, would have encouraged him to proceed.

Our discussion of CESALPINO's classificatory effort would not be complete if we did not listen to what he himself has to say with regard to it in the concluding chapters of book I. As we have already seen, he tries in these three chapters to justify the choice of the characters on which his classification is based by pointing out that they are taken from those parts in which the two most important functions of the plant are located. These two functions are "nutrition" and "reproduction". "Nutrition" has in CESALPINO's vocabulary nearly the same meaning as it has in our own, but "reproduction" is for him exclusively the reproduction by means of seeds, and as there are plants that do not produce seeds, this function is a less general one than "nutrition", which obviously can nowhere be missed. For this reason the characters taken from the parts that perform an important function in the process of "reproduction" come after those taken from parts that are of importance in the process of "nutrition".

CESALPINO is of opinion that in order to carry out the processes comprised under the term "nutrition" the plant is provided with a root and a leafy shoot, the function of the root being the absorption of food from the soil, and that of the leafy shoot the assimilation of the absorbed food and the distribution of the products of this assimilation process over the various parts. Root and shoot show a corresponding differentiation: in one group of plants they are stronger and harder ("substantia habitior et durior"), whereas in the other group they are thinner and weaker. In this way he tries to justify the division of the plant kingdom in woody plants and herbaceous ones.

In view of the gradual transition between the woody condition and the herbaceous one, it is difficult to see how a critical investigator like CESALPINO could have acquiesced in this division. His own groups 6 and 17, the woody and the herbaceous *Leguminosae* differ in this point only, so that it seems impossible that he can have overlooked their near affinity. The unfortunate choice of this difference as a base for the main division, shows how easily's one's judgment may be led astray by traditional conceptions. CESALPINO obviously accepted this time-hallowed division because apparently nobody had as yet found it necessary to test the value of this distinction. However, we should not blame CESALPINO too severely, not only because it would take more than a century before a system was evolved in which this almost entirely illusory difference was dropped, but also because, strange enough, the idea to use this vague difference for the subdivision of one of the major groups, viz. the *Angiospermae*, was revived in recent times, e.g. in the classifications proposed by HALLIER.

CESALPINO's division of his two main groups is said to be based on those parts in which the second important function of the plant is located, viz. the fruits and seeds. The plants that produce no seeds, are dealt with at the end of the herbaceous plants: they represent the lowest grade of differentiation. The existence of woody plants without seeds could, of course, not shake this belief, as such plants were at that time unknown. It is worth while to see in which way these seedless plants are dealt with. Cesalpino begins with a group of plants whose vegetative parts are similar to those of the seedplants. These are the *Filicales*, *Equisetum* and the genera *Botrychium* and *Ophioglossum*. Then he passes on to the *Hepaticae* and the *Musci*, and these are followed by the *Lichenes* and the *Algae*, in which the genus *Lemna* and also some *Coelenterata* (*Corallium*, *Alcyonium*) are included, and he ends his enumeration with the *Fungi*. On the whole, therefore, a quite natural arrangement.

The differences in the fruits and seeds on account of which the two groups of seedplants are subdivided, are found in the number, the position and the general aspect of these parts, but Cesalpino does not bind himself to the sequence in which these attributes are here enumerated. Particulars with regard to this subdivision will be given further on and in the key to Cesalpino's groups that is given at the end of this paper, but before discussing them, it seems appropriate to draw the attention to the fact that he occasionally used characters that have nothing to do with the fruits and seeds. Examples are the subdivision of the herbaceous *Leguminosae* on account of the presence or absence of tendrils, the subdivision of the plants with trilocular several-seeded fruits according to the presence or absence of swollen underground parts, the subdivision of the *Compositae* in three groups according to the general aspect of the capitula, and the creation of the group "*Junci*" (*Typha*, *Cyperus*, *Juncus*), which is dealt with in an appendix to the treatment of the *Gramineae*, on account of the uninodal flowering shoots. Cesalpino certainly was not so dogmatic as Sachs would induce us to believe!

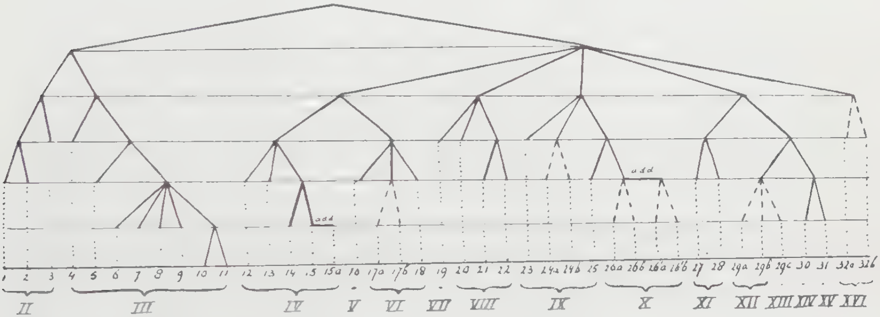
With regard to the groups 1–3 of the woody plants Cesalpino remarks that they generally differ from the groups 4–11 by the position of the embryo in the seed. In the groups 1–3 the rootlet would, as a rule, be turned away from the hilum, in the groups 4–11 towards the latter. This, at least, is what his words imply, but because he regarded one-seeded fruits that are not provided with a distinct cavity, as seeds, the position of the rootlet is not everywhere described with regard to the hilum but sometimes, viz. in the one-seeded fruits, with regard to the base of the fruit.

That it occurred to Cesalpino to look towards the embryo when he found that the proper characters of the fruit and seed, viz. their number, position and general aspect, proved insufficient, is perhaps not so unexpected. A century later Ray came by the same trend of thought to the discovery of the two main types of embryo structure that are found in the *Angiospermae* viz. that with two cotyledons and that with a single one. However, as stated above, the position of the embryo inside the seed and with regard to the axis of the fruit is also of considerable importance, but before Cesalpino's idea could bear full fruit, this position had to be more sharply defined.

However, the first subdivision of the woody plants is not based in the first place on the position of the embryo, but on the presence of one or more seeds per fruit. The next subdivision is in both cases founded on the position of the fruit with regard to the parts for which Cesalpino uses the term "flos", which I have translated by "blossom" because it has a much wider meaning than is expressed by the term "flower". "Flos" comprises in Cesalpino's delimitation all those parts by which the future fruits or groups of fruits originally are surrounded, with the exception of ordinary leaves. He uses the term therefore in flowers for the perianth with the stamens and in flower-like inflorescences for all accessory parts, i.e. for bracts, perianths and stamens, and with regard to the latter it is of no importance whether they are arranged round the pistils or in separate flowers In the capitula of the *Compositae* the "blossom" comprises the involucre as well as the bracts, perianths and stamens of the individual flowers, and in bisexual catkins it comprises the bracts as well as the male flowers. A male catkin too falls under the notion "flos". It can, of course, hardly be expected that plants which are brought together on account of the position of such extremely heterogeneous parts will form natural groups, and they certainly will not do so when they are sufficiently numerous. Group 3 may serve as an example of such a heterogeneous group (see the list of genera included in this group in the catalogue of the groups given at the end of this paper).

The woody plants with several-seeded fruits are subdivided in the same way, and the second group, that with the "blossom" at the base of the pistil, is once more subdivided on account of the position the seeds occupy inside the fruit. Those in which they are inserted on one or more longitudinal placentae are arranged according to the number of these placentae or, as Cesalpino expressed it, according to the number of branches of the placenta. In most cases the number of placentae corresponds with the number of fruit cells, but this is no general rule, for in group 7 we encounter an *Apocynacea*, i.e. a plant with a bilocular ovary, as well as *Salix* and *Populus*, which are provided with a unilocular ovary with two parietal placentae. The group with several placentae is split once more, viz. according to the consistency of the "fruit", in *Coniferae*, where it is a cone, and "*Mali*" (*Pyrus*, *Citrus*, *Punica*), where it is fleshy. The cone of the *Coniferae* was therefore regarded by Cesalpino as a single fruit with several cells, each provided with a "branch of the longitudinal placenta".

The main division of the herbaceous plants rests on the number of cells per fruit or on the number of fruits formed within the same perianth or involucre, and corresponds therefore more or less with the division of the several-seeded woody plants provided with longitudinal placentae according to the number of the latter, but whereas this difference was used in the woody plants in the third place, it comes here first. It leads to the distinction of five main groups, the last one being that without fruits or seeds. Three of the four others are subdivided according to the presence of one or more seeds in each cell, and in case there is but one seed per cell, by the presence or absence of an open space between the seed and the pericarp. The fourth group is somewhat inconsistently subdivided according to the presence of four or more than four mericarps or fruits inside the "blossom". The group with the four mericarps is the one that is subsequently split according to the position the embryo occupies in the nucule, in *Boraginaceae* and *Labiatae*. The other one proves to be a very strange mixture, for it contains the *Compositae* as well as families like the *Ranunculaceae*, *Nymphaeaceae*, *Alismataceae*, the herbaceous *Rosaceae*, the *Geraniaceae* and *Malvaceae*. The next subdivision is based on the presence or absence of "blossom" on the individual fruits, and leads to the splitting off of the *Compositae*, the remaining plants being subdivided according to the presence of one or more than one seed per fruit or mericarp. The two groups that are formed in this way are still rather heterogeneous.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II III IV V VI VII VIII IX X XI XII XIII XIV XV XVI

Fig. 1. Graphic representation of CESALPINO's system showing the successive divisions. The final groups are indicated by arabic numbers; the books in which they are described by roman ones. The abbreviation *add* leads to groups that do not fit into the system, but are dealt with by CESALPINO in connection with the group by which they are preceded.

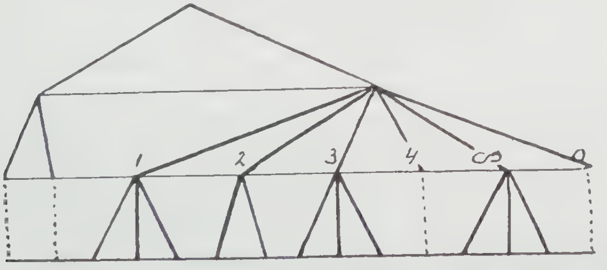


Fig. 2. Graphic representation of CESALPINO's system based on the abstract of the latter given by LINNÉ. The arabic figures indicate the number of fruits or fruit cells fromed by a flower or flower-like inflorescence. The roman numbers indicate the 'classes' which LINNÉ supposed to have been accepted by CESALPINO; they correspond to the books II–XVI.

Fig. 1 graphically represents the structure of CESALPINO's classification. For comparison I have added in fig. 2 a diagram based on the abstract of his system given by LINNÉ. According to the latter

Cesalpino would have divided the plant kingdom into 15 "classes", of which the first two belong to the woody plants and the rest to the herbaceous ones. The 13 "classes" of the herbaceous plants would have been obtained by a first division into six groups according to the number of fruits or fruit cells per flower or flowerlike inflorescence followed by a further division of some of these primary groups. Linné's exposition rests on the erroneous assumption that each of the books II to XVI contains a "class". In reality the number of Cesalpino's groups is more than twice as large, and they corespond in no way with the division in books, which apparently owes its origin to Cesalpino's wish to split the work in a number of more or less equal parts. Maybe the subject was originally treated by him in a course of lectures; in that case each of the books would contain the contents of a single lecture. In the diagram founded on my own interpretation of Cesalpino's classification I have indicated in which of the books his groups are dealt with, and this shows that some of the books deal with a comparatively large number of them, e.g. book III with 8, book IV with 4, but that the majority deals with 1–3 groups, and the books XII and XIII together with a single one.

The groups of higher order arrived at by the first two or three divisions can but rarely be regarded as natural ones. The artificiality of the main division, i.e. the division in woody and herbaceous plants, has already been discussed, but the results of his second division are hardly more satisfactory. The two main groups of the woody plants are both of a very heterogeneous composition, and the same applies to at least three of the five main groups in which the herbaceous plants are divided, viz. the first and second, respectively consisting of the groups 12–18 and 19–22, and the fourth, which contains the groups 27–31. In our eyes the whole set of consecutive divisions is no more than an artificial key to the 32 final groups which, themselves are for a large part quite acceptable. However, it is obvious that Cesalpino did not regard his divisions in this way, otherwise he would not have felt the need to justify the choice of the characters on which they rest. In this respect his classification can not be regarded as a success, but we should not forget that it would still take a long time before, starting with the distinction of the *Monocotyledones* and the *Dicotyledones* and via the separation of the *Gymnospermae* from the *Angiospermae*, for the seedplants a set of more or less satisfactory classes was evolved; even now the delimitation of the latter is in several instances far from convincing.

I will end this paper with a summary of Cesalpino's classification. I give it in the form of an identification key, for it is in this form, as I have pointed out, that its real significance is to be seen. Part of the terms used by Cesalpino have been replaced by their modern equivalents. The meaning of the term "blossom" has been explained above.

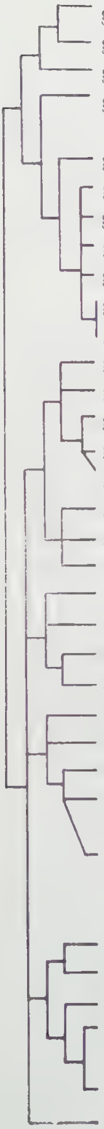
The key is followed by a survey of Cesalpino's groups. The way in which they are arrived at, is indicated by the use of brackets.

Key to CESALPINO's groups

1*a*. Woody plants
2*a*. with one-seeded fruits
3*a*. with superior "blossom"
4*a*. with coriaceous pericarp . . . . group 1
4*b*. with osseous endocarp . . . . group 2
3*b*. with inferior "blossom" . . . . group 3
2*b*. with several-seeded fruits (eventually with pseudocarps containing several seedlike fruits)
5*a*. without "blossom" or with superior "blossom" group 4
5*b*. with inferior "blossom"
6*a*. seeds inserted at the bottom of the fruit cavity group 5
6*b*. seeds inserted on one or more longitudinal placentae
7*a*. one placenta . . . . group 6
7*b*. two placentae . . . . group 7
7*c*. three placentae . . . . group 8
7*d*. four placentae . . . . group 9
7*e*. more than four placentae
8*a*. fruit a cone . . . . group 10
8*b*. fruit fleshy . . . . group 11
1*b*. herbaceous and suffruticose plants
9*a*. fruit unilocular
10*a*. fruit one-seeded
11*a*. fruit not crowned with a persistent calyx and not not enclosed within a perianth or involucre group 12
11*b*. fruit crowned with a persistent calyx . . . . . group 13
11*c*. fruit enclosed within a perianth or involucre
12*a*. rootlet turned away from the hilum or from the base of the fruit. . . . . group 14
12*b*. rootlet turned towards the hilum . . . . . . group 15
add.: plants with a uninodal flowering shoot ("*Junci*") . . . . group 15*a*
10*b*. fruit several-seeded
13*a*. fruit a berry . . . . group 16
13*b*. fruit a legume . . . . group 17
α. plants with tendrils
β. plants without tendrils
13*c*. fruit with a central placentae . . . . group 18
9*b*. fruit bilocular
14*a*. fruit a double caryopsis . . . . group 19
14*b*. fruit cells with a single free seed . . . . group 20
14*c*. fruit cells with several seeds
15*a*. dissepiment perpendicular to the plane of symmetry group 21
15*b*. dissepiment in the plane of symmetry . . . . group 22
9*c*. fruit trilocular
16*a*. fruit a triple caryopsis . . . . group 23
16*b*. fruit cells with a single free seed . . . . group 24
α. plants with latex
β. plants without latex

16*c*. fruit cells with several seeds
17*a*. subterranean parts not bulbous . . . . group 25
17*b*. subterranean parts bulbous . . . . group 26
α. "blossom" inferior
β. "blossom" superior
add.: "*Liliaceae*" without bulbs . . . . group 26*a*
α. "blossom" inferior
β. "blossom" superior
9*d*. fruit quadrilocular or more than 4 fruits inside an involucre or perianth
18*a*. fruit quadrilocular (splitting into 4 nucules)
19*a*. rootlet pointing to the top of the nucule . . . group 27
19*b*. rootlet pointing to the base of the nucule. . . group 28
18*b*. more than 4 fruits inside an involucre or perianth
20*a*. each fruit originally provided with "blossom" group 29
α. "blossom" on all fruits ligulate
β. "blossom" marcescent
γ. "blossom" ligulate on the marginal fruits only
20*b*. fruits with a common "blossom" (i.e. formed inside a perianth)
21*a*. fruits with a single seed . . . . group 30
21*b*. fruits with several seeds . . . . group 31
9*e*. without fruit and seed . . . . group 32
α. plants provided with root and shoot
β. plants without root and shoot.

CATALOGUE OF CESALPINO'S GROUPS



group 1. *Quercus*, *Castanea*
group 2. *Juglans*
group 3. *Prunus*, *Myristica*, *Palmae*, *Musa*
group 4. *Ficus*, *Morus*, *Opuntia*, *Sambucus*, *Hedera*, *Viscum*, *Oleaceae* p.p., *Rosa*, *Rubus*
group 5. *Vitis*, *Arbutus*, *Zizyphus*
group 6. woody *Leguminosae*
group 7. *Salicaceae*, *Periploca*
group 8. *Buxus*, *Myrtus*
group 9. *Verbenaceae*
group 10. *Coniferae*
group 11. "*Mali*": *Pyrus*, *Citrus*, *Punica*
group 12. *Valeriana*, *Daphne*, *Jasminum*
group 13. *Osyris*, *Valerianella*
group 14. *Chenopodiaceae*, *Urticaceae*, *Cannabinaceae*
group 15. *Gramineae*
group 15*a*. "*Junci*": *Cyperus*, *Sparganium*, *Typha*, *Juncus*
group 16. *Cucurbitaceae*, *Solanaceae* p.p., some *Liliaceae*, *Arum*
group 17. herbaceous *Leguminosae:* α. with tendrils, β. without tendrils
group 18. *Caryophyllaceae*, *Primulaceae*
group 19. *Umbelliferae*
group 20. *Mercurialis*, *Agrimonia*, *Poterium*, *Rubia*, *Galium*
group 21. *Cruciferae*
group 22. *Scrophulariaceae*, *Solanaceae* p.p., *Plantago*, *Pirola*, *Potamogeton*
group 23. *Thalictrum*
group 24. *Euphorbiaceae:* α. with latex; β. without latex
group 25. *Hypericum*, *Campanula*
group 26. *Liliiflorae:* α. with superior ovary (*Liliaceae*); β. with inferior ovary (*Iridaceae*, *Amaryllidaceae*)
group 26*a*. *Liliiflorae* and similar plants without bulbs: α. with superior ovary (*Aloë*, *Lilium*); β. with inferior ovary (*Iris*, *Agave*, *Orchidaceae*)
group 27. *Boraginaceae*
group 28. *Labiatae*
group 29. *Compositae:* α. *Cichorieae;* β. *Artemisia;* γ. *Anthemideae*
group 30. *Ranunculaceae* with one-seeded fruits, *Alisma*, *Geranium*, *Potentilla*
group 31. *Ranunculaceae* with follicles, *Nymphaea*, *Oxalis*, *Gossypium*
group 32. *Cryptogamae:* α. *Filicales*, *Equisetum*, *Botrychium*, *Ophioglossum;* β. *Hepaticae*, *Musci*, *Lichenes*, *Algae* (incl. *Lemna*, some *Coelenterata*), *Fungi.*

ERISMADELPHUS

BY

R. W. J. KEAY (Kew) and F. A. STAFLEU (Utrecht)

(Received Dec. 1st, 1952)

Erismadelphus Mildbr. is remarkable because it is the only African genus of the *Vochysiaceae*, a family represented in tropical America by no less than 5 genera and 180 species. *Erismadelphus* was discovered in 1913 by Prof. J. Mildbraed and has hitherto been represented by only one species: *E. exsul* Mildbr.

Recent examination of the African collections has, however, revealed the existence of two other taxa. Unfortunately the type of *E. exsul* (Mildbraed s.n. from Elon, French Cameroons) was destroyed at Berlin during the 1939–45 war and no duplicates or cotypes are known to exist. In response to an enquiry Prof. Mildbraed, to whom we are very grateful, informed one of us that in his view *Corbisier* 1362 from Eala in Belgian Congo was identical with his original type. Prof. Mildbraed and Keay have, in fact, together examined *Corbisier* 1362 in the Herbarium of the Jardin Botanique de l'Etat at Bruxelles through the courtesy of Prof. Robyns. Duplicates of *Corbisier* 1362 are at Kew and Paris, they agree in every respect with Mildbraed's original description and figure and we therefore propose that this specimen be adopted as the neotype (lectotype).

Erismadelphus Mildbr. and *Erisma* Rudge belong to the tribe *Erismeae* Dumort. of the *Vochysiaceae*. This tribe is characterized by a unilocular practically inferior ovary and by an indehiscent fruit enclosed by enlarged calyx-lobes. *Erismadelphus* differs from *Erisma* mainly by the presence of a complete set of five petals, by the fertile stamen standing in the symmetry plane at the base of the third petal (see diagram in fig. 2) and by the calyx-lobes enlarging after anthesis. These enlarged lobes are the wings of the fruit and make it resemble the fruits of *Dipterocarpaceae*. It is apparent that *Erismadelphus*, with its five petals and its symmetrical flowers, has — morphologically speaking — simpler flowers than *Erisma*. Its place in the *Erismeae* is therefore analogous to that of *Salvertia* in the tribe *Vochysieae* Dumort. and it is interesting to observe these parallel relationships in the two tribes of the family *.

ERISMADELPHUS Mildbr. Bot. Jahrb. **49**: 547–551. 1913; Chevalier & Russel, Compt. Rend. Acad. Sci. **188**: 565. 1929.

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* cf. F. A. Stafleu, Acta Botanica Neerlandica **1**: 223. 1952, also in Med. Bot. Mus. Utrecht **108**: 223.

Arbores. Folia opposita stipulata; lamina coriacea pennicostata, nervis secundariis subparallelis haud numerosis. Flores in cincinnis pedunculatis dispositi, bracteis sessilibus persistentibus, cincinnis iterum in paniculam dispositis. Calyx semisuperus profunde quinquefidus, laciniis omnibus persistentibus et post anthesim excrescentibus, quarta (torsione postica) basi incrassata et in duo calcaria obtusa superposita producta. Petala quinque subaequalia longe unguiculata, cum calycis laciniis alternantia. Stamen unicum (rarius 2) petalo mediano antepositum. Staminodia 1–3. Ovarium inferum uniloculare, ovulum unicum anatropum includens. Fructus indehiscens, calycis laciniis excrescentibus longe alatus.

Type-species: *Erismadelphus exsul* Mildbr.

Distribution: Two species in West tropical Africa (cf. fig. 3).

KEY

1*a*. Petioles 7–15 mm long, leaves 8–25 cm long and 3½–11 cm wide, bracts 7–9 mm long and 8–10 mm wide 2

b. Leaves sessile, 6–8 cm long and 2½–3½ cm wide, bracts 4–5 mm long and wide. 1. **E. sessilis** Keay & Stafl. sp. nov.

2*a*. Leaves 3½–7 cm wide, entirely glabrous; leaf-base always cuneate; lateral nerves only somewhat more prominent than the very prominent secondary venation beneath . . . . 2*a*. **E. exsul** Mildbr. var. **exsul**

b. Leaves 7–11 cm wide, with petiole, midrib and main lateral nerves tomentellous beneath; leaf-base usually cordate or subcordate, rarely cuneate; lateral nerves much more prominent than the secondary venation beneath . . . . 2*b*. **E. exsul** Mildbr. var. **platyphyllus** Keay & Stafl. var. nov.

1. **Erismadelphus sessilis** Keay & Stafl. sp. nov. (fig. 1).

Ab *E. exsule* Mildbr. foliis sessilibus minoribus angustioribus, bracteis et floribus minoribus, laciniis calycis brevioribus apice obtusis differt.

Arbor. Ramuli juveniles tomentelli. Stipulae subovatae incrassatae ½–1 mm longae, eae foliorum oppositorum basibus linea prominula ramulum transiente connexis. Folia sessilia, lamina elliptica nonnunquam oblanceolato-elliptica, basi cuneata, apice obtusata, 6–8 cm longa et 2½–3½ cm lata, supra glabra nervis haud prominentibus; costa nervique laterales subtus puberuli etiam senectute; lamina ipsa subtus inter nervos primum puberula deinde glabrescens; nervi laterales utrinque 6–9 subtus cum costa valde prominentes; rete venularum subtus subprominens.

Paniculae thyrsoideae, partibus juvenilibus tomentellis. Flores in cincinnis plerumque bifloribus, bracteis late reniformi-cordatis circa 4–5 mm longis et latis, nervo mediano conspicuo. Calycis laciniae exteriores oblique et late lanceolatae, apice obtusae, circa 6 mm longae et 2–2½ mm latae; laciniae anteriores oblongae, apice rotundatae vel obtusae circa 6 mm longae et 2½–3 mm latae, lacinia postica oblonga. Petala calycis lacinias superantia obovata, apice rotundata vel obtusa, in alabastris circa 5 mm longa et 2½ mm lata. Stamen unicum (rarius 2) filamento pilosulo circa 1½ mm longo; connectivum crassum oblongum apice subincrassatum et subtruncatum circa 1½ mm longum, antheris circa ¾ mm longis. Staminodia 1 vel 2 parvula claviformia. Stylus ¾–1 mm longus, stigmate capitato. Fructus ignotus.

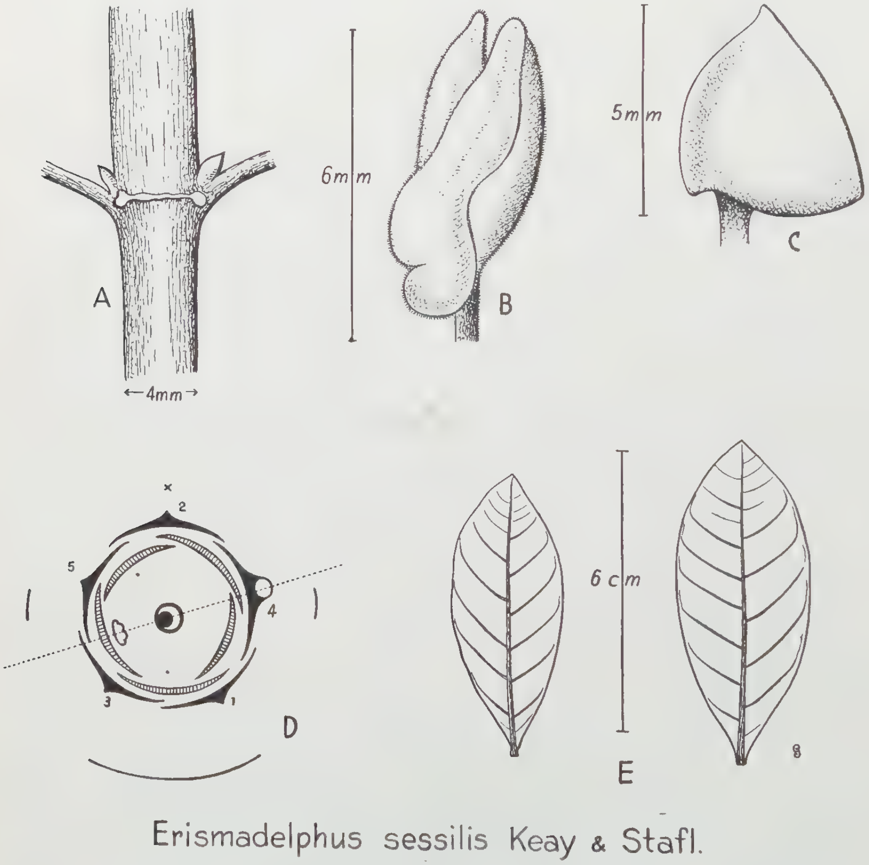

Fig. 1. *Erismadelphus sessilis* Keay & Stafl. A. stipular ridge; B. flower-bud; C. bract; D. diagram; E. leaves.

Holotype: Georges Le Testu 5559, Gabon, Kembélé (Haute Ngounyé), fl. 4 Oct. 1925: in herb. P (specimen unicum).

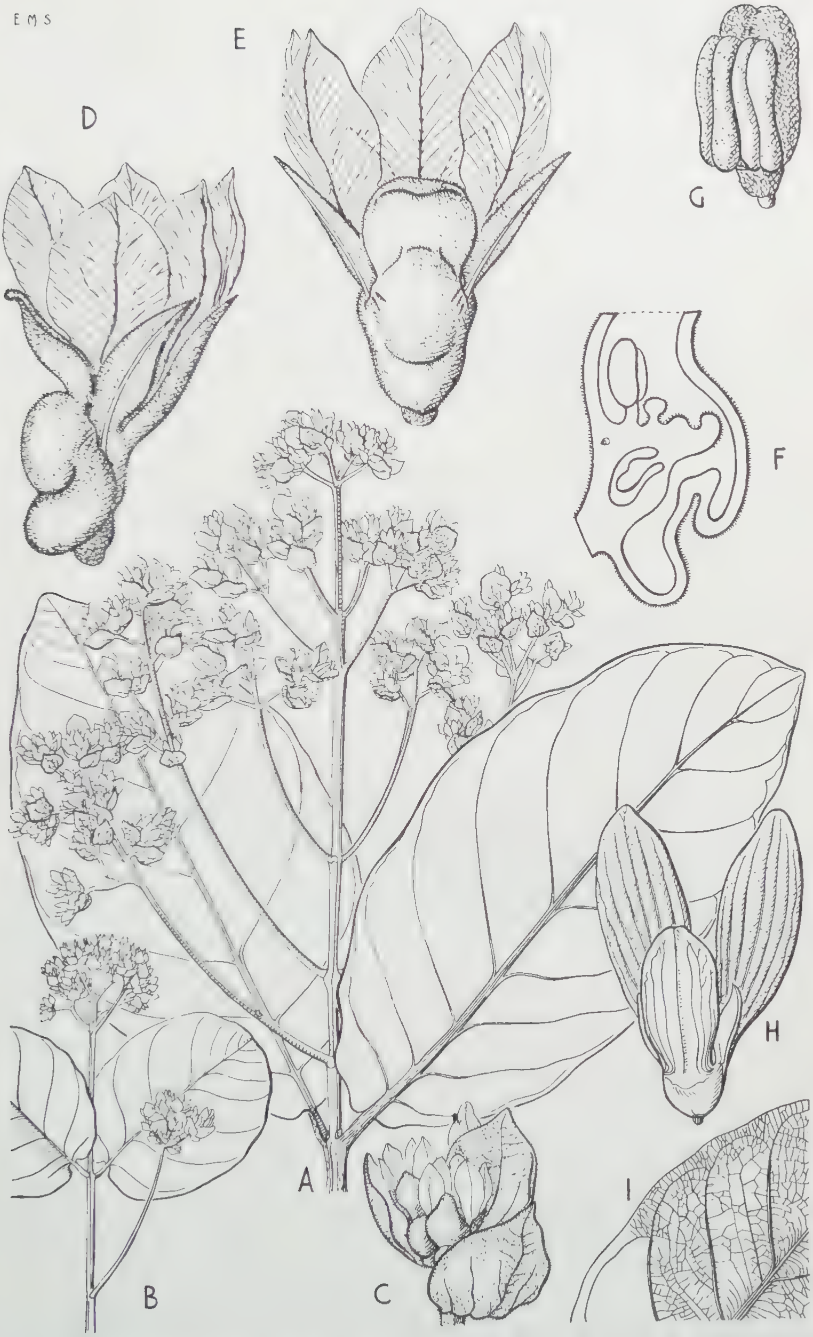

Fig. 2. *Erismadelphus exsul* Mildbr. var. *platyphyllus* Keay & Stafl. A. inflorescence; B. young leaves; C. cincinnus and bracts; D & E. adult flower; F. longitudinal section of the flower; G. stamen; H. fruit; I. secondary nervation of the leaf.

2. **Erismadelphus exsul** Mildbr. Bot. Jahrb. **49**: 547–551. *pl. 1.* 1913; Engler & Drude, Vegetation der Erde **9** (3^1): 831. *pl.392.* 915. *Erismadelphus baudoni* A. Chev. Compt. Rend. Acad. Sci. **188**: 565. 1929.

a. var. **exsul**

Lectotype (neotype): *Corbisier* 1362, Eala, Belgian Congo, 1932: in herb. BR; dupl.: K,P. *Holotype* of *E. baudoni* A. Chev.: *A. Baudon* in herb. *Chevalier* 34066: P.

Distribution: West Equatorial Africa (cf. fig. 3).
Gabon: Haut-Ogooué, *A. Baudon* in herb. *Chevalier* 34066, fl. Dec. 1927 (P).
French Congo: Fort Rousset, *Aubréville* 231, fl. 27 Oct. 1945 (P).
Belgian Congo: Eala, *Corbisier* 1362, fl. 1932 (BR, K,P); Eala, J. *Lebrun* 533, fl. 1930 (BR, P); Yangambi, *Louis* 9964, fl. (BR, K).

b. var. **platyphyllus** Keay & Stafl. var. nov. (fig. 2).

Ab var. *exsule* foliis basi subcordatis vel alte cordatis, petiolis costis nervisque lateralibus subtus tomentellis differt.

Holotype: *Georges Le Testu* 8593, Poungwé, Gabon, 18 Dec. 1930: in herb. P., dupl.: K.

Distribution: Nigeria, Cameroons and Gabon (cf. fig.3).
Nigeria: Calabar Prov. Forestry Compound, no. 1 Leopard Town, *M. Robson* FHI 1027, fl. 24 Apr. 1936, fr. 24 June 1936 (FHI, FHO, K); same locality, *Okpala* & *Amachi* FHI 24302, lvs & seedling 2 Sep. 1949 (FHI, K); same locality, *J. O. Amachi* FHI 24313, lvs & seedlings 15 Sep. 1951 (B, FHI, K, P, U); Calabar Prov. Oban, *G. C. R. Gray* 6/10, fr. 19 Nov. 1934 (K); Ogoja Prov. Ikom, *J. H. Mackay* s.n. (FHO); Ogoja Prov. Ikom, Cross River, *R. Catterall* 40, fl. & fr. Aug. 1934 (K); Ogoja Prov. Ikom, Ukpon Forest Reserve, *J. D. Kennedy* 3128 (BM).
British Cameroons: Kumba Division, branch road to Bombe, *J. Dundas* FHI 8489, st. 16 Nov. 1946 (FHI, FHO); Kumba Division, Victoria-Kumba road, mile 41.5, *M. C. Ejiofor* FHI 29315 L, fl. 5 Apr. 1951 (FHI).
Gabon: Haute Waka, *Georges Le Testu* 2194, fl. Nov. 1916 (Herb. Le Testu); Poungwé, région de Lastoursville, *Georges Le Testu* 8593, fl. 18 Dec. 1930 (K, P); Haute Ngounyé, Les Echiras, *Georges Le Testu* 5813, fr. 14 Dec. 1915 (P, herb. Le Testu, photogr. in FHO); Equata, Forêt littorale, *M. Bernard* SRF 509, lvs 3 Aug. 1951 (K); same locality, *M. Bernard* SRF 539, fl. 25 Sep. 1951 (K); Mondah, *M. Estasse* SRF 581, lvs. 18 Oct. 1951 (K).
Ecology: Rain-forest tree.

The known distribution of these taxa is shown in fig. 3. It is interesting to observe that all three taxa are known to occur in Gabon within approximately 100 km. of each other. *E. sessilis* is at present known by only one specimen, but the specimens of the two varieties of *E. exsul* are more numerous and show distinct areas. *E. exsul* var. *exsul* extends from the French Cameroons and Gabon southwards and eastwards to Yangambi where only the one taxon is known, and var. *platyphyllus* extends northwards and westwards to S.E. Nigeria where again only the one taxon is known.

We are much indebted to M. Georges Le Testu who loaned to Kew specimens from his own rich herbarium for our examination and kindly asked the Section de Recherches Forestières in Gabon to obtain further material. MM. Bernard and Estasse (of the Service

des Eaux et Forêts) who collected this new material in Gabon note that *Erismadelphus exsul* var. *platyphyllus* is very abundant in littoral forest where as many as 40 trees per hectare may be found.

In conclusion we wish to acknowledge our gratitude to Prof. H. HUMBERT and his staff at the Laboratoire de Phanérogamie, Muséum d'Histoire Naturelle, Paris, for it was there that we were able to revise the genus. The second author acknowledges gratefully the financial support given to him by the Centre National de la Recherche Scientifique on the suggestion of the Netherlands Organization of Pure Research (Z.W.O.).

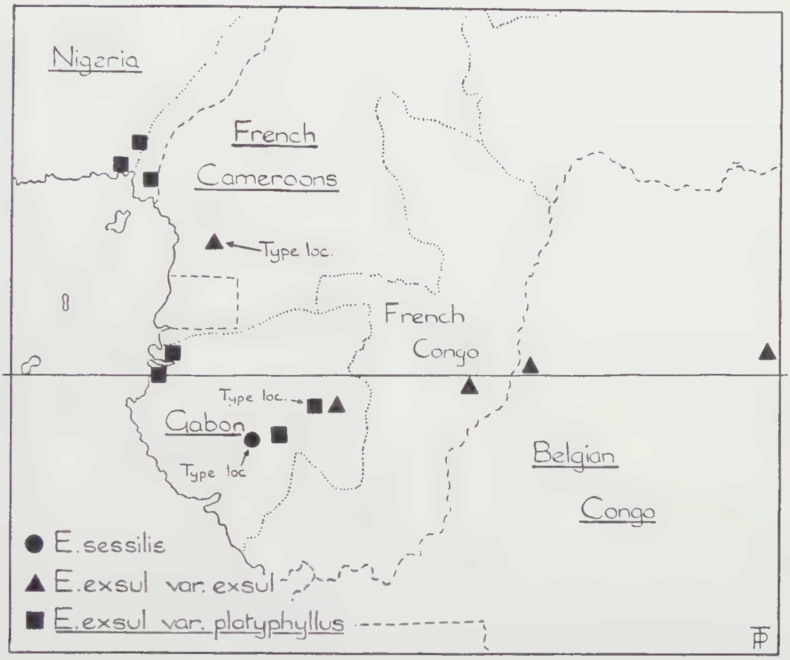

Fig. 3. Geographical distribution of the species and varieties of *Erismadelphus*.

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„Overdruk uit het Nederlandsch Kruidkundig Archief, Deel 57, 1950”.

Koninklijke Nederlandsche Botanische Vereeniging

(Opgericht 15 Augustus 1845).

BESTUUR IN 1947

Prof. Dr W. H. ARISZ, *Voorzitter.*
Dr J. LANJOUW, *Ondervoorzitter.*
Prof. Dr J. HEIMANS, 1*ste Secretaris.*
Mevr. Dr H. C. BELS–KONING, 2*e Secretaresse.*
Dr P. JANSEN, *Penningmeester.*

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Dr J. LANJOUW, *Ondervoorzitter.*
Prof. Dr J. HEIMANS, 1*ste Secretaris.*
Mej. Dr A. JAARSVELD, 2*e Secretaresse.*
Dr P. JANSEN, *Penningmeester.*

VERSLAGEN OVER HET JAAR 1946.

JAARVERSLAG van de eerste secretaris over 1946.

Met grote voldoening kan geconstateerd worden, dat na de benarde tijden, die achter ons liggen, de Vereniging in 1946 weer vrijwel geheel tot het normale leven kon terugkeren. Zowel de algemene ledenvergaderingen als de vergaderingen der commissies konden weer als vroeger gehouden worden en werden door vele leden bijgewoond.

Naast het verheugende feit dezer opleving staat echter het verlies, dat onze Vereniging leed, doordat een tweetal corresponderende leden, een onzer ereleden en een 7-tal gewone leden ons door de dood ontvielen. Het bericht bereikte ons namelijk, dat Prof. Dr A. H. R. BULLER van de Universiteit van Manitoba en Prof. Dr M. A. A. GUILLIERMOND te Parijs, beiden corresponderend lid der Vereniging sinds 1935, zijn overleden.

Een zeer zwaar verlies trof onze Vereniging op 1 September door het plotseling heengaan van ons erelid Dr W. H. WACHTER.

Het is hier niet de plaats om uitvoerig in te gaan op zijn vele verdiensten, daar er in het Nederlandsch Kruidkundig Archief een speciaal artikel aan hem zal worden gewijd, maar toch mag hier nog wel gewezen worden op het zeer vele en goede werk, dat hij zo lange jaren voor onze Vereniging, die hem zo nauw aan het hart lag, heeft gedaan. Het moge ons een voldoening zijn, dat wij hem op de Herdenkingsvergadering ter gelegenheid van het 100-jarig bestaan der Vereniging nog het erelidmaatschap hebben kunnen aanbieden.

Van de gewone leden ontvielen ons door de dood Mej. Dr E. G. C. TALMA, Dr A. RANT, Ir G. A. HEUBEL, Dr M. C. E. STAKMAN, Ir N. VAN POETEREN, DR G. L. FUNKE en G. J. A. VAN DE WOUW. Zij allen hebben, elk op zijn manier, de botanische wetenschap helpen bevorderen. Moge hier speciaal nog gememoreerd worden het vele werk gedaan door Ir VAN POETEREN op het gebied der phytopathologie en door Dr FUNKE op dat der plantenphysiologie en in de laatste tijd op dat van de experimentele plantensociologie.

Benoemd werden gedurende 1946 een 48-tal nieuwe leden, waaronder 33 gewone leden, 5 gecombineerd-leden en 10 student-leden, terwijl 7 gecombineerd-leden de wens te kennen gaven als gewoon lid te willen toetreden. Een 14-tal personen bedankte intussen met ingang van 1947 voor het lidmaatschap, zodat op 1 Januari van dit jaar de Vereniging telt 15 corresponderende leden, 4 ereleden en 471 leden, te weten 364 gewone leden, 51 gecombineerd-leden en 56 student-leden, wat een toename van het totale ledenaantal sinds 1 Januari 1946 met 24 personen betekent.

Na het periodiek aftreden van de Voorzitter, Dr V. J. KONINGSBERGER, werd op 27 Januari Dr W. H. ARISZ in diens plaats benoemd. In de Permanente Commissies werden verder de volgende nieuwe leden gekozen: Commissie voor de Bescherming van de Wilde Flora, in de vacature G. A. BROUWER: V. WESTHOFF; in de vacature ontstaan door het overlijden van Dr J. P. THIJSSE: Dr J. HEIMANS; Commissie voor de Biosociologie enz., in de vacature van de Voorzitter, Dr A. A. PULLE: Dr A. SCHEYGROND; Commissie voor de Phytopathologie, in de vacature Mej. Dr J. C. WENT: Mej. Dr C H. KLINKENBERG en in de vacature Mej. L. C. DOYER: Dr J. W. M. ROODENBURG. De aftredende leden in de Commissie van Redactie voor het Nederlandsch Kruidkundig Archief (W. H. WACHTER), in de Commissie van Redactie voor het Recueil (Dr K. ZIJLSTRA), in de Commissie voor de Bibliotheek en het Herbarium (Dr TH. WEEVERS), in de Commissie voor het Floristisch Onderzoek (Ir J. L. VAN SOEST) en in de Subcommissie voor het Zuiderzee-onderzoek (Dr G. KRUSEMAN) werden herkozen, terwijl bovendien de laatstgenoemde subcommissie met twee leden werd aangevuld, nl. met de heren H. W. E. CROOCKEWIT en J. MELTZER.

Het Bestuur vergaderde drie maal, nl. op 30 Maart, 28 September en 21 December, telkens te Amsterdam ten huize van de Penningmeester.

Een drietal algemene ledenvergaderingen werd gehouden en wel op 27 Januari te Utrecht, op 1 September te Amsterdam en op 16 November wederom te Utrecht. Op de eerste dezer vergaderingen, de jaarvergadering, hield Dr KONINGSBERGER een voordracht getiteld: „Zeventig jaar antibiose, penicilline". De vergadering van 1 September, de Indische dag, was speciaal gewijd aan voordrachten van een aantal uit Indië gerepatrieerde leden. Voor de vergaderingen en werkzaamheden der Commissies kan verwezen worden naar de afzonderlijke verslagen.

De steeds verder doorgevoerde specialisatie in de verschillende onderdelen der botanie maakt het gewenst de leden meer gelegenheid te geven speciale onderwerpen in afzonderlijke Commissievergaderingen te bespreken. Het zal hier veelal onderwerpen betreffen, die voor beoefenaars van andere onderdelen der botanie niet van direct belang zijn. In een aantal Commissies was dit reeds mogelijk. Als gevolg van hierover gehouden besprekingen kon in de vergadering van 27 Januari een Commissie voor Plantenphysiologie in het leven worden geroepen en in die van 1 September een Commissie voor de Plantensystematiek en de Plantengeographie. Tot leden van deze Commissies werden benoemd, in de Commissie voor de Plantenphysiologie: Dr W. H. ARISZ, Mej. Dr A. M. HARTSEMA, Dr A. W. H. VAN HERK, Dr T. H. VAN DEN HONERT, Mej. Dr A. KLEINHOONTE, Dr V. J. KONINGSBERGER en Dr J. W. M. ROODENBURG; in de Commissie voor de Plantensystematiek en de Plantengeographie: Mej. Dr CH. H. ANDREAS, Dr J. TH. HENRARD, Dr H. J. LAM, Dr J. LANJOUW, Dr S. J. VAN OOSTSTROOM en Dr A. A. PULLE.

Op 16 November werd behalve de ledenvergadering een vergadering belegd van het Bestuur te zamen met de voorzitters en secretarissen van een aantal Commissies ter bespreking van de wijze, waarop een goede samenwerking tussen de Commissies onderling kan worden bevorderd.

Door het feit, dat de Vereniging het praedicaat Koninklijke verwierf en door het oprichten van de reeds eerder genoemde twee nieuwe Commissies, waren enige statutenwijzigingen nodig. Deze werden op de ledenvergadering van 1 September voorgesteld en goedgekeurd. Tegelijkertijd werden op deze vergadering de reglementen der beide nieuwe Commissies vastgesteld.

De bibliotheek der Vereniging werd in de loop van 1946 opnieuw gerangschikt en opgesteld in de ervoor speciaal ingerichte localiteit van het Rijksherbarium. Zij is thans weer geheel toegankelijk. Ook de voorraad der tijdschriften en andere uitgaven werd gerangschikt en opgesteld. Deze werkzaamheden, benevens het bijwerken van de kaartcatalogus geschiedde door de technisch ambtenaar aan het Rijksherbarium, de heer H. J. VAN HATTUM, die met de zorg voor de bibliotheek belast is.

Van groot belang is het feit, dat de ruilverbindingen met een aanzienlijk aantal buitenlandse verenigingen en instituten hersteld konden worden en dat zodoende de tijdens de oorlog ontstane hiaten in de tijdschriftseries voor een groot deel konden worden aangevuld. Een belangrijke hoeveelheid der in de bezettingstijd verschenen delen van Archief en Recueil was nog niet naar het buitenland verzonden kunnen worden en kon nu tot herstel der ruilverbindingen worden aangewend. Te betreuren is, dat na de bezettingstijd noch van het Archief, noch van het Recueil tot nu toe een deel kon worden uitgegeven. Personeelsgebrek en moeilijkheden met onvoldoend geschoold personeel bij de drukker zijn hiervan grotendeels de oorzaak. Hopelijk zullen zeer binnenkort echter enige delen van beide tijdschriften kunnen verschijnen, nl. deel 54 en 55 van het Archief en deel 40 van het Recueil. Genoemde moeilijkheden veroorzaakten ook stagnatie in het zetten van het eerste deel van de Flora Neerlandica.

Enige malen waren de voorzitter of de eerste secretaris aanwezig bij besprekingen met andere verenigingen en instituten. Zo o.a. vertegenwoordigde de Voorzitter op uitnodiging van de Nederlandsche Chemische Vereeniging ons bij een oriënterende bespreking over het onderwerp „Vakbonden op natuurwetenschappelijk gebied" en de eerste secretaris op een bijeenkomst ter bespreking van de eventuele oprichting van een Stichting voor Hydrobiologisch Onderzoek van T.N.O., terwijl hij eveneens de Vereniging vertegenwoordigde op het Congres van Leraren in de Wiskunde, Natuurkunde Scheikunde en Biologie op 30 October te Amsterdam.

Oegstgeest, 1 Januari 1947.
De eerste Secretaris,
S. J. VAN OOSTSTROOM.

VERSLAG van de Commissie van Redactie van het Recueil des Travaux botaniques néerlandais over 1946.

Het jaar 1946 was evenals 1945 een jaar van afwachten. Volgens de mededelingen van de drukker zou het papier van deel 40 in het voorjaar toegewezen kunnen worden en zou er dan direct een begin kunnen worden gemaakt met het afdrukken van deel 40, dat reeds in 1943 gezet is. Het schijnt, dat het papier pas in Augustus door de drukker ontvangen is. Desalniettemin verscheen het deel niet in 1946, ondanks het feit, dat in November de laatste hand aan titel en omslag was gelegd, en op het omslag werd medegedeeld, dat het deel in 1946 was uitgegeven. Inmiddels is er kopie voor deel 41 naar de drukker gezonden en van een gedeelte van deze kopie zijn proeven ontvangen. Na die tijd stagneert alles.

De secretaris en de voorzitter van de redactiecommissie hadden op 28 September een bespreking met het bestuur en met de redactie van het Nederl. Kruidkundig Archief over een verzoek van een aantal leden der K.N.B.V. om het formaat der tijdschriften te veranderen en het Recueil in afleveringen uit te geven.

Baarn, 31 Dec. 1946.

De secretaris der
Redactie-Commissie,
A. PULLE.

VERSLAG van de Commissie van Redactie voor het Nederlandsch Kruidkundig Archief over 1946.

De Commissie leed een zeer zwaar verlies door het overlijden van haar secretaris Dr W. H. WACHTER, die bijna 30 jaar lang de uitgave van het Archief op buitengewone wijze verzorgde. In de vacature werd voorzien door de benoeming van ondergetekende.

Na Deel 53, dat in December 1943 werd uitgegeven, verscheen geen nieuwe jaargang meer. Nadat het eindelijk, dank zij de bemoeiingen van de voorzitter, gelukt was papiertoewijzing te verkrijgen, ontstonden nieuwe moeilijkheden, doordat de drukker niet over voldoende materiaal en geschoold personeel beschikte.

Het Gedenkboek, dat als Deel 55 zal verschijnen, is reeds lang gereed om afgedrukt te worden, doch door deze moeilijkheden nog steeds niet verschenen. Deel 54, waarin de verslagen en mededelingen over 1944 komen, is bijna geheel gezet en zal na Deel 55 het licht zien. Daar het Gedenkboek geen jaarlijkse verslagen zal bevatten, worden deze over 1945 en 1946 in Deel 56 opgenomen.

Het is te hopen, dat de moeilijkheden nu spoedig opgelost zullen zijn en de verslagen en mededelingen van onze vereniging weer regelmatig kunnen verschijnen.

Nijmegen, Januari 1947.

De Secretaris,
J. H. KERN.

VERSLAG van de Commissie voor de Bibliotheek en het Herbarium over 1946. 1)

Een buitengewoon ernstig verlies leed de Commissie door het plotselinge overlijden van Dr W. H. WACHTER, die sinds 1919 haar ziel was; hij was als secretaris degene, die, als geen ander, de belangen van bibliotheek, herbarium en archief bewaakte; zijn plaats werd ingenomen door Ir J. L. VAN SOEST. Het herbarium werd uitgebreid door een dankbaar aanvaarde schenking van de familie van wijlen Prof. Dr L. H. SIERTSEMA (1114 vnl. Nederlandse Phanerogamae); van V. WESTHOFF werd nog één plant ontvangen.

In 1946 werden zendingen aan de volgende personen uitgeleend: Mr FRANCIS DROUET (18 Cyanophyceae), Dr H. R. HOOGENRAAD (58 Cruciferae), JOH. JANSEN (2 Rosaceae), J. H. KERN (2 Alismataceae), W. MEIJER (127 Hepaticae), H. PRELL (7 Cyperaceae), TH. REICHGELT (103 Cyperaceae), Ir J. L. VAN SOEST (16 Guttiferae), Dr W. H. WACHTER (218 Papaveraceae), V. WESTHOFF (124 Gramineae).

Uit vorige jaren zijn nog ongeveer drieduizend planten aan verschillende personen uitgeleend.

Voor de bibliotheek was het aantal bezoekers 12 en uitgeleend werden 227 werken.

Buiten de door het toegenomen ruilverkeer ontvangen werken, werden aan de bibliotheek geschonken meest proefschriften en overdrukken: M. J. ADRIANI, Dr C. A. BACKER, Dr J. G. B. BEUMÉE (4), Dr J. BRAUN BLANQUET, D. DEINUM, W. VAN DIJK, CHR. J. GORTER, G. J. M. A. GORTER (11), Dr P. JANSEN, Dr W. K. M. KARSTENS, Prof. Dr J. KLIKA (9), Dr Ir A. W. KLOOS, W. KRUYT, Dr J. KUIJPER, Prof. Dr H. J. LAM, W. LÜDI (6), I. LUYTEN, H. M. MOLDENKE (5), Dr J. VAN OVERBEEK (2), Prof. Dr P. VAN OYE (20), Dr F. VAN DER PAUW, Dr C. A. REINDERS—GOUWENTAK, C. J. P. SPRUIT, Dr C. G. G. J. VAN STEENIS (4), J. DE TEMPE, Dr W. H. WACHTER, Dr E. C. WASSINK (5), Dr Ir S. J. WELLENSIECK (19), V. WESTHOFF (2), A. H. A. DE WILLIGEN, H. C. D. DE WIT. Ook een aantal overdrukken vloeide toe als bijlagen van de Mededelingen van de Vereniging, in Nederlands-Indië verschenen.

'S-Gravenhage, 3 Januari 1947.

De Secretaris,
J. L. VAN SOEST.

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1) De bij dit verslag behorende Aanvullingslijst op de gedrukte Catalogus der Kon. Ned. Bot. Ver. blijft in het Archief van de Secretaris der Commissie berusten, totdat een nieuwe Catalogus kan worden uitgegeven.

VERSLAG van de Commissie voor het Floristisch Onderzoek over 1946.

Er werden dit jaar 2 vergaderingen uitgeschreven, beide zeer druk bezocht. De voornaamste mededelingen zullen te zijner tijd in het Kruidkundig Archief worden opgenomen.

Een succesvolle excursie werd begin Augustus gehouden in de omgeving van Ootmarsum.

Voor 1947 wordt voorgesteld een excursie te houden in de omgeving van Coevorden.

De Secretaris,
P. Jansen.

VERSLAG van de excursie der K.N.B.V. naar Ootmarsum en omgeving van 1 tot 9 Augustus 1946.

Ootmarsum was het uitgangspunt van de Unio 1946. De voorzitter van onze Commissie voor het Floristisch Onderzoek van Nederland, Dr Ir A. W. Kloos Jr had een geschikt pied-à-terre gevonden in Hotel de la Poste van de heer J. H. A. Beukers, dat ons wel niet kon bergen, maar waar toch onze maaltijden verzorgd werden, terwijl wij hier en daar in 't dorp sliepen.

13 en 14 Juni had Kloos al reeds een verkenningsexcursie gemaakt, bij welke gelegenheid 7 kwartierhokjes werden geïnventariseerd, te weten: M7. **28.** 11, 13, 12/21, 23, 31/32, 43 en **38.** 21, Bovendien werden nog een paar losse notities gemaakt in M7. **18.** 33, **28.** 12, 21, 31, 32, 34. De ingevulde lijsten zagen er niet gek uit. Trouwens, een aantal deelnemers aan de Unio kende de streek al enigszins, doordat zij er op eigen gelegenheid al eens waren geweest. De excursies van de Ned. Bot. Ver. waren in die buurt nooit verder gekomen dan Albergen bij Almelo in Juli 1870. Wel was er in Juni 1905 een „Plantenkaartjes-excursie" geweest, maar daarvan zijn de resultaten nooit gepubliceerd.

Zo begon de Unio dan op 1 Aug. 1946 te Almelo, waar we bij het station *Galinsoga quadriradiata* troffen. Per auto werden we — dat waren van Dijk, Heimans, Joh. Jansen, Kern, Kloos, van Ooststroom, Piet en Sloff — naar Ootmarsum gebracht, waar we P. Jansen troffen. Later kwamen nog Boer, Brand en de Bruin.

Die 1e Augustus werd, de traditie getrouw, het „woonhok" M7 **28.**32 nog geïnventariseerd en een deel van **28.**14, d.i. in de richting van Oud-Ootmarsum. Daarbij toonde P. Jansen ons *Festuca loliacea* van hetzelfde slootkantje, waar hij de plant ± 20 jaar te voren ook gevonden had.

Vrijdag 2 Augustus gingen we in de voormiddag de weg op naar Albergen, waarbij we in M7. **28**.32 en 31 voornamelijk de oligocene leemgroeve tegen de Kuipersberg bekeken. We vonden daar weer de aardige vegetatie van *Fragaria vesca fruct. alb.*, die KLOOS reeds bij zijn voor-excursie had gezien.

's Middags wandelden we de weg naar Denekamp tot de kruising van de Tiggelter beek. Hierbij werden M 7.**28**.41 en 42 geïnventariseerd.

Zaterdag 3 Aug. werd bestemd voor een wandeling, die de hele dag in beslag nam, nl. naar de bronnen van de Springendalse beek. Hierbij werden M7.**28**. 14, 12, 11 en 13 bekeken. Opmerkelijk was hier de *Montia*, die we over drie kwartierhokken verspreid in verschillende beekloopjes vonden, aansluitend bij de vondst van KLOOS in Juni. Vroegere noteerders hebben deze planten hetzij als *Montia minor*, hetzij als *M. rivularis* genoteerd. Het leek ons alles *Montia lamprosperma*. Bij de verificatie van het herbarium-materiaal uit Leiden kon KLOOS de aanwezige Ootmarsumse planten eveneens tot *M. lamprosperma* brengen.

Zondag 4 Augustus bekeken we eerst de Ootmarsumse Ringwal Oost in M7.**28**.32. Hierna begon de wandeling langs de zuivelfabriek naar het water-reservoir in M7. **28**.34. Daar begon een wegje zuidwaarts, waarlangs KLOOS bij de voor-excursie in een aardappelakker *Equisetum silvaticum* had gevonden. Deze groeide er nog, volop zelfs en allerminst in de schaduw. Ook de *Equisetum arvense* in die akker was vreemd. Er waren er bij, die habitueel aan *E. arvense* × *silvaticum* deden denken, wat achteraf toch niet juist gebleken is. Verder gaande inventariseerden we M7.**28**.43 en kwamen zo in het broekland bij de oude kooi. Hier kon ons medelid PIET de zeer zeldzame Syrphide *Eristalomyia cryptarum* bemachtigen.

In dit broekterrein misten we wel de oude accomodatie, toen we excursionnisten bij ons hadden met auto's. Nu moesten we voor de lunch teruglopen naar Ootmarsum, ruim drie kwartier gaans, met het plan om 's middags naar hetzelfde terrein terug te keren.

Dat deden we via de Denekamper weg, waarbij we door het ontgonnen Tilligter Broek kwamen en zo tevens in M7.**28**.42.44 konden noteren. Langs de weg, die wij volgden, konden we het Kooibroek niet verder inkomen, zodat we met een omwegje door M7.**38**.21 terug keerden. In dit terrein was ons zowel 's morgens als 's middags opgevallen de fraaie vegetatie van *Agrimonia odorata*.

Maandag 5 Aug. maakten we weer een hele-dag-excursie naar het bronnenland van de Mosbeek bij hoeve Paus-Klein-Jan achter Oerbekke. Deels wandelend, deels fietsend, deels per bus gingen we eerst naar Vasse, onderweg noterend in M7.**27**. 24 en 21. Daarbij viel op *Leersia* aan de plas bij de watermolen van Hazelbekke. Van Vasse uit liepen we gezamenlijk langs de Hooiweg door M7.**17**.43. 44 en 42 naar het bronnenland, dat we zonder de aanwijzingen van de heer PIET wellicht niet gevonden zouden hebben. Het zag er nog zeer fraai uit met de vegetatie van *Pinguicula*, *Parnassia*, *Vaccinium Oxycoccus*, *Orchis* e.d. Echter zat er nogal wat *Phragmites* in, dat op den duur de andere planten wel wat zal overgroeien. En dan is de hoge rand rond het bronnenland reeds in cultuur. Niettemin, we genoten voor het moment en rekten het verblijf nog door, uitgestrekt tussen de *Juniperus* aan de hoge rand, ons meegenomen boterhammetje te verorberen. De fietsers keerden, toen we tenslotte opgebroken waren, langs dezelfde weg als 's morgens terug. De wandelaars tippelden al hokkend door M7.**27**. 22 en **28**. 31. terug.

Dinsdag 6 Aug. trokken we er op uit naar 't kanaal Nordhorn-Almelo, sommigen per fiets, anderen te voet. Onderweg hokkend in M7. **28**. 34 en **38**. 12 en 14 noteerden we langs de weg reeds *Dianthus deltoïdes*. Langs het kanaal in **38**. 23 en 24 kwam deze volop, tezamen met andere planten uit het dal van de Dinkel: *Euphorbia Cyparissias*, *Thymus Chamaedrys*, *Agrimonia Eupatoria* e.d. De Hunenborg in M7. **38**. 24 en 22 viel tegen. Planten van zonnige stroomdalkanten, die HEIMANS daar in 1934 kon noteren, als *Galium verum*, *Thymus Chamaedrys* waren er niet meer te vinden; het geheel was dichtgegroeid. Terugkerend langs de zuidkant van het kanaal, vonden we daar aan de oever op een paar plekken *Leersia* en verder de pas kort tevoren ontdekte *Alisma lanceolatum*, die er tezamen met *Alisma Plantago* groeide. Beide soorten waren goed te onderscheiden. Ten eerste aan de bladeren, die bij *A. lanceolatum* belangrijk smaller zijn. Dan aan de stijl, die bij *A. lanceolatum* kort, bij *A. Plantago* belangrijk langer is en aan de vorm van de vrucht. Maar het meest opvallende kenmerk is reeds de bloeitijd. *A. lanceolatum* heeft 's morgens open bloemen, *A. Plantago* 's middags. Dit bleek hier langs het kanaal volkomen op te gaan. We hadden nog een buitenkansje: op twee plaatsen vonden we de nog slechts twee maal gevonden en in Groningen door opzettelijke kruising verkregen bastaard van beide *Alisma's*.

We gingen langs het kanaal de Agelerbrug voorbij, steeds de zuidoever houdend, tot het Paris-bosje op de grens van M7. **38** 31 en 32. We troffen er *Paris quadrifolia* aan (ook in 5-bladige exx.) *Sanicula*, *Viola Riviniana*, *Rhamnus catharctica*, *Circaea lutetiana*, *Lysimachia nemorum*, *Primula elatior*, enz.

Woensdag 7 Aug. gingen we met een merkbaar gereduceerd gezelschap noordwaarts, richting Neuenhaus. Eerst aan de oostzijde van de straatweg door M7. **28**. 23 en 24, waarbij we langs de Poelbeek, de Vlasbeek en de Hollandse Graven kwamen. Het fraaist was een tredplantengezelschap langs een van de zandwegen met *Scirpus setaceus*, *Radiola*, *Cicendia* en *Peplis*.

Na de middag splitsten we ons: Kloos en Joh. Jansen gingen per fiets er op uit richting Denekamp, waar ze in M8. **21**. 34 en **31**. 11, 12, 13 verschillende Dinkelplanten konden noteren en ook *Solanum Dulcamara flor. alb.* zagen.

Heimans, Piet en Sloff noteerden in M7.**28**. 32, 31, 33, **27**. 44 en 42. Het beekdal in het laatste hokje viel tegen.

Donderdag 8 Aug. was Sloff nog alleen over. Hij vulde de voorhanden notities in M7. **28**. 34, 33, **27**. 44, **37**. 22, 24, 23 wat aan om vervolgens langs de noordkant van het kanaal in **37**. 41 en 42, **38**. 31. 14 te hokken. Het bosje tegenover het twee dagen te voren bekeken Paris-bosje, plaatselijk bekend als „Achter de Voorst” bleek nagenoeg hetzelfde aspect te hebben als zijn overbuurman: *Paris*, *Sanicula*, *Primula*, *Circaea*, *Viola Riviniana*.

Vrijdag 9 Aug. was ook voor Sloff de laatste dag, waarop de Springendalse beek en omgeving nog eens verder bekeken werd en de grenshokjes M7. **18**. 31, 32, 33, 34, 43 en 44 werden doorlopen. Deze leverden eigenlijk alleen nog een rijke plek *Montia lamprosperma* op. De noordelijke spreng van de Sprengendalse beek, die nu bezocht werd, viel tegen: afgetrapt door de vele daar rond kamperende padvinders was er weinig te beleven.

Zo werd deze laatste dag eigenlijk een teleurstelling. Maar thuisgekomen, viel dat toch weg: Ootmarsum was ons door het aantrekkelijke landschap uitstekend bevallen en de verzamellijst voor M7 vertoonde het lang niet onaardige aantal van 560 soorten en variëteiten van phanerogamen en vaatcryptogamen.

Een aantal mossen en paddestoelen werd bovendien genoteerd. En die zullen ook in de I.V.O.N.-albums worden opgenomen. In dit verslag gaan wij ze echter voorbij. Doordat noch bryologen, noch mycologen van de partij waren, hebben we natuurlijk van alles over het hoofd gezien, zodat een lijst alleen een verkeerd beeld kan geven van wat er groeit. Ook phytosociologen ontbraken ditmaal: het blijft dus bij een floristische opsomming.

Alvorens het overzicht der genoteerde planten op te maken, eerst iets over hetgeen uit de bezochte streek bij de I.V.O.N. bekend was. Jammer genoeg ontbreekt de gelegenheid na te gaan wat de oudste floristen rond Ootmarsum al verzameld hadden.

Zo vinden we als eerste notities voor het blad M7 de hoklijstjes van de Plantenkaartjesexcursie van 12 tot 14 Juni 1905 door Blijdenstein, van Breemen, Lako, Mej. Rust en Wachter. Bij deze gelegenheid werden op het traject Denekamp-Ootmarsum-Albergen-Almelo in de door ons bezochte streek geïnventariseerd de kwartierhokken M7. **27**. 43, 44, **28**. 14, 23, 31, 32, 33, 34, 41, 42, 43, 44, **37**. 12, 13, 14, 21, 22, 31, **38**. 11, 12, 21, 22. Dat leverde 309 soorten op.

De volgende maand, om precies te zijn op 8 Juli 1905, inventariseerde BLIJDENSTEIN het hokje M7. **37**. 43, waarvoor hij 68 soorten aantekende, waarvan 5 nieuw.

Dat was in de eerste tijd van de kwartierhok-inventarisatie volgens het Systeem GOETHART en JONGMANS. Toen dat begon te stagneren, is LAKO verder gegaan Overijssel te inventariseren voor zijn Cartografische flora van die provincie, welke als manuscript op het Rijksherbarium berust. Daar zijn de gegevens van de hierboven genoemde hoklijsten in verwerkt, maar ook andere, eigen notities, die niet van in het I.V.O.N.-archief berustende lijsten afkomstig zijn. Alle vermeldingen van LAKO zijn in de I.V.O.N.-albums overgenomen, wat voor het gebied in kwestie nog 45 nieuwe soorten opleverde.

Schrijver dezes maakte in 1929 enkele notities in M7. **28**.12 bij de sprengen van de Sprengendalse beek: geen nieuwe soorten.

In 1931 bezocht KRUSEMAN de hokjes M7. **38**, 23 en 24, wat 176 soorten opleverde, waarvan 36 (vnl. planten langs het kanaal Almelo—Nordhorn) nieuw waren.

Pinksteren 1934 was KRUSEMAN weer in de streek: inventarisatie van M7. **37**. 32, 33, 34 met 199 soorten, waarvan 19 nieuw.

In datzelfde jaar 1934 bezocht HEIMANS van Denekamp uit het kanaal Nordhorn—Almelo en de streek benoorden Oostmarsum: M7. **18**. 33, **28**. 11, 21, **38**. 14, 24 en 31 met 216 soorten, waarvan 25 nieuw.

Juni 1936 was KRUSEMAN opnieuw in de streek. Deels met Mevr. M. C. KRUSEMAN-JANSEN, deels alleen inventariseerde hij M7. **17**. 44, **18**. 33, 34, **28**. 12, **38**. 13, 41, 42, 44, terwijl hij nog sociologische opnamen maakte in **27**. 11, **28**. 14, 31 en **38**. 42. Dat leverde 277 soorten op, waarvan 17 nieuw.

Daarna kwamen nog wat losse aanvullingen: enkele notities van F. P. JONKER uit 1937 voor M7. **38**. 32: 1 nieuwe soort. Enkele sociologische opnamen van W. H. DIEMONT uit 1939 voor M7. **17**. 44, **27**. 32, **28**. 11, 12, **38**. 32, 42: 4 nieuwe soorten. Twee gedeeltelijke inventarisaties door TH. WEEVERS van M7. **38**. 33 en 34 uit 1939: 6 nieuwe soorten. Een sociologische opname voor M7. **38**. 23 door M. F. MÖRZER BRUINS en V. WESTHOFF uit 1941: geen nieuwe soorten.

Zo waren er eind 1945 voor het door ons bezochte gebied 467 soorten bekend.

Bij de voor-excursie naar Ootmarsum op 13 en 14 Juni 1946 maakte Kloos, zoals al eer vermeld, min of meer volledige inventarisatie van M7. **18**. 33, **28**. 11, 12, 13, 21, 23, 31, 32, 34, 43 en **38**. 21. De verzamellijst daarvan komt tot 306 soorten, waarvan 28 nieuw.

Daarna kwam dan onze excursie, die in de 45 bezochte hokjes van het kaartblad M7 in totaal 548 plantensoorten (resp. ondersoorten) telde, waarvan 53 geheel nieuw waren.

Voor de 4 hokjes van M8, die bezocht werden, waren dat 267 soorten. Uit oudere opgaven (Plantenkaartjes-excursie 1905, Heimans 1934 en J. J. Piet 1937) waren er 203 soorten bekend. Wij konden daar 115 soorten aan toevoegen, zodat het bezochte deel van M8 nu op 318 soorten kwam. Op enkele uitzonderingen na waren deze reeds uit M7 bekend of zijn deze daar door ons ook gevonden.

In totaal kwamen we voor het bezochte gebied van M7 en M8 aan oude en nieuwe opgaven op 600 phanerogamen en vaatcryptogamen, hierna vermeld. Slechts 38 daarvan werden niet door Kloos bij zijn voor-excursie of door ons allen bij de Unio genoteerd. Wij hebben dus wel een goede neus gehad!

In de overzichtslijst worden de andere genoteerde cryptogamen niet vermeld; die opsomming zou te onvolledig zijn geworden. Wel zijn de notities daarvan in de betrokken I.V.O.N.-albums opgenomen.

Bijlage.

PLANTENSOORTEN UIT DE IN 1946 BEZOCHTE KWARTIERHOKJES.

Acer Pseudoplatanus M7. **17**. 43, **27**. 44, **28**. 31, Achillea Millefolium 43 in M7, 3 × in M8, A. Ptarmica 32 × in M7, 4 × in M8, Acorus Calamus M7. **28**. 34, **37**. 41, 42, **38**. 14, 32 (d.i. vnl. langs het kanaal Nordhorn-Almelo), Adoxa Moschatellina wel bij vroegere invent., Aegopodium Podagraria 21 in M7, 3 × in M8, Aesculus Hippocastanum M7. **28**. 13, 32, 43, Aethusa Cynapium M7. **17**. 43, **28**. 23, 32, 34, 41, 42, Agrimonia Eupatoria M7. **38**. 23, 24, 32, M8. **31**. 13 (d.i. alle langs het kanaal N.-A.), Agrimonia odorata (nieuw) M7. **28**. 44, Agrostemma Githago wel bij vroegere invent., Agrostis alba (= A. stolonifera) 39 × in M7, 4 × in M8; P. Jansen verzamelde van deze soort *fm. prorepens*, *gigantea* en *natans*, A. canina 13 in M7, 2 in M8, A. vulgaris (= A. tenuis) 41 × in M7, 4 × in M8; ex. in herb. Jansen-Wachter, Aira caespitosa (= Deschampsia caespitosa) 13 × in M7, 2 × in M8, A. discolor (= D. setacea) wel in Cartogr. Flora van Overijssel door Lako, Aira flexuosa (= D. flexuosa) 25 × in M7, 2 × in M8, Ajuga reptans 12 × in M7, Alchemilla arvensis M7. **27**. 42, **28**. 13, 31, 41, Alisma lanceolatum (nieuw) M7. **38**. 14, 32, M8. **31**. 12; ex. in herb. Kloos, A. lanceolatum × Plantago (nieuw) M7. **38**. 14, 32; ex. in herb. Kloos, Alisma natans (= Elisma natans) M7. **28**. 12, 21, 34, Alisma Plantago-aquatica 20 × in M7, 3 in M8, Alisma ranunculoïdes (= Echinodorus ranunculoïdes) wel bij vroegere invent., Alnus glutinosa 36 × in M7, 1 × in M8, A. incana (nieuw) M7. **17**. 42, **28**. 33, Alopecurus fulvus (nieuw) M8. **21**. 34, **31**. 12, A. geniculatus

11 × in M7, 1 × in M8, A. pratensis M7. **28.** 32, 34, 41, Amelanchier canadensis wel bij vroegere invent., Anagallis arvensis M7. **28.** 32, Andromeda Polifolia wel bij vroegere invent., Anemone nemorosa M7. **28.** 31, **38.** 32, Angelica silvestris 34 × in M7, 1 × in M8, Anthemis arvensis M7. **17.** 42, 43, 44, **18.** 34, 43, **28.** 12, 23, Anthoxanthum odoratum 29 × in M7, 4 × in M8, A. Puelii (= A. aristatum) 23 × in M7, 2 × in M8, Anthriscus silvestris M7. **28.** 12, Apera Spica-venti 16 × in M7, Arenaria serpyllifolia M7. **38.** 14, 23, Arnoseris minima M7. **17.** 43, 44, **27.** 44, **28.** 12, 13, 23, 31, **37.** 23, Arrhenatherum elatius 10 × in M7, 1 × in M8, Artemisia campestris (nieuw) M7. **38.** 23, A. vulgaris 14 × in M7, 3 × in M8, Asplenium Ruta-muraria wel bij vroegere inv., Athyrium Filix-femina 26 × in M7, 3 × in M8, Atriplex latifolia (= A. hastata) M7. **17.** 43, **28.** 12, 23, 31, 34, 41, 43, M8. **21.** 34, A. patula M7. **18.** 31, **28.** 11, 31, 32, 34, **37.** 24, Avena caryophyllea (= Aira caryophyllea) M7. **38.** 14, 23, 24, M8. **31.** 11, 12, 13, A. fatua (nieuw) M7. **28.** 31, A. flavescens (= Trisetum flavescens), wel bij vroegere invent., A. praecox (= Aira praecox) M7. **27.** 42, **28.** 34, **38.** 23, 24, M8. **31.** 11, 13, A. sativa (nieuw) M7. **17.** 43, 44, **27.** 22, 42, 44, **28.** 33, 41, 43.

Batrachium hederaceum (= Ranunculus hederaceus) M7. **28.** 14, B. heterophyllum (= Ranunculus aquatilis) M7. **28.** 31, B. trichophyllum (= Ranunculus trichophyllus) (nieuw) M7. **28.** 23, 24, M8. **31.** 12, Bellis perennis 20 × in M7, 2 × in M8, Berula angustifolia (= Sium erectum) 13 × in M7, 1 × in M8, Betula sp. 41 × in M7, 2 × in M8, Bidens cernuus M7. **38.** 21, B. tripartitus 33 × in M7, 1 × in M8, Blechnum Spicant 12 × in M7, Brassica Napus wel bij vroegere invent., B. oleracea M7. **28.** 32, 42, Briza media M7. **38.** 14, 23, 24, 31, 32, M8. **31.** 13, Bromus mollis 15 × in M7, 3 × in M8, B. racemosus M7. **28.** 22, B. sterilis M7. **28.** 12, Butomus umbellatus M7. **38.** 32, M8. **21.** 34, **31.** 12.

Calamagrostis epigeios M7. **38.** 23, 32, M8. **31.** 12, 13, C. lanceolata (= C. canescens) 12 × in M7, Callitriche hamulata (nieuw) M7. **28.** 12, M8. **21.** 34, C. spec. M7. **17.** 42, **28.** 12, 31, 42, 43, **38.** 21, Calluna vulgaris 39 × in M7, 3 × in M8, id. fa decumbens M7. **28.** 11, **37.** 41, Caltha palustris 13 × in M7, Campanula rotundifolia 22 × in M7, 3 × in M8, Cannabis sativa wel bij vroegere invent., Capsella Bursa-pastoris 29 × in M7, 3 × in M8, Cardamine amara wel bij vroegere invent., C. pratensis 10 × in M7, 2 × in M8, Carex acuta (= C. gracilis) M7. **27.** 42, **28.** 24, 41, 42, 44, M8. **21.** 34. C. acutiformis (nieuw) M7. **28.** 44, C. canescens M7. **28.** 13, 14, 24, **38.** 21, C. demissa Hornem. (nieuw) M7. **17.** 42, **28.** 22, 24, C. disticha M7. **28.** 14, 24, 41, 44, C. echinata M7. **17.** 42, **27.** 44, **28.** 11, 12, 13, 14, 33, 44, C. elongata M7. **27.** 42, M7. **28.** 12, 22, 24, 42, **38.** 21, 22, 24, M8. **31.** 12, C. flava ssp. Oederi (= C. serotina Mér.) M7. **28.** 12, 42, C. glauca (= C. flacca) M7. **38.** 32, C. hirta 10 × in M7, 3 × in M8, C. leporina 10 × in M7, C. muricata (nieuw) M7. **38.** 14, M8. **21.** 34, C. pallescens (nieuw) M7. **28.** 31, C. panicea M7. **17.** 42, **28.** 12, 22, 44, **38.** 23, 32, M8. **21.** 34, C. paniculata M7. **27.** 22, **28.** 14, C. pilulifera M7. **17.** 44, **18.** 31, **27.** 22, **28,** 11, 12, 23, **38.** 23, 32, C. Pseudocyperus M7. **27.** 22, **28.** 44, **37.** 23, **38.** 14, 21, 22, 24, C. remota 13 × in M7, C. riparia M7. **28.** 42, 44, **38.** 23, C. rostrata (= C. inflata) M7. **17.** 42, **28.** 12, 13, 22, 24, M8. **21.** 34, C. stricta (= C. reticulosa Peterm.) (nieuw) M7. **38.** 22, C. vesicaria M7. **28.** 12, 42, 44, **38.** 21, 24, C. vulgaris (= C. stolonifera) M7. **17.** 42, **28.** 12, 13, 14, 22, 44, **38.** 21, Carpinus Betulus M7. **27.** 24, **28.** 14, 32, 41, M8. **31.** 12, Castanea sativa M7. **28.** 12, Centaurea Cyanus 26 × in M7, C. Jacea sens. ampl. 10 × in M7, 4 × in M8, Cerastium arvense M7. **28.** 42, M8. **21.** 34, **31.** 13, C. glomeratum M7. **28.** 12, 31, 42, C. semidecandrum M7. **28.** 31, C. triviale (= C. caespitosum) 32 in M7, 4 × in M8, Chaerophyllum temulum 17 × in M7, 1 × in M8, Chelidonium majus M7. **17**. 43, **28**. 32, **38**. 13, Chenopodium album 33 × in M7, 1 × in M8, C. polyspermum M7. **17**. 43, **28**. 14, 31, 32, 34, 44, **38**. 22, Chrysanthemum inodorum (= Matricaria inodora) M7. **28**. 31, 34, 42, 43, 44, **38**. 22, C. Leucanthemum 21 × in M7, 3 × in M8, C. Parthenium (nieuw) M7. **28**. 12, 32, 34, C. segetum M7. **28**. 31, 43, **38**. 12, Chrysosplenium alternifolium wel bij vroegere inv., Cicendia filiformis M7. **28**. 22, Cicuta virosa M7. **37**. 41, 42, **38**. 12, 14, 23, 31 (d.i. langs het kanaal Nordhorn-Almelo), Circaea lutetiana M7. **28**. 14, 32, **38**. 13, 14, 32, Cirsium anglicum (= C. dissectum, nieuw) M7. **17**. 42, C. arvense 23 × in M7, 4 × in M8, C. lanceolatum (= vulgare) 9 × in M7, 1 × in M8, C. palustre 36 × in M7, 1 in M8, C. p. fl.alb. (nieuw) M7. **27**. 42, **28**. 21, 42, Comarum palustre 13 in M7, Convallaria majalis M7, **18**. 33, **28**. 12, Convolvulus arvensis M7. **28**. 31, C. sepium (= Calystegia sepium) 15 × in M7, 1 × in M8, Cornus sanguinea M7. **38**. 32, Corrigiola litoralis wel bij vroegere inv., Corydalis claviculata 10 × in M7, 1 × in M8, Corylus Avellana 19 × in M7, 1 × in M8, Corynephorus canescens M7. **18**. 33, **27**. 21, **28**. 12, 14, **37**. 42, Crataegus monogyna 14 × in M7, C. Oxyacantha 9 × in M7, Crepis virens (= C. capillaris) 9 × in M7, 2 × in M8, Cuscuta Epithymum M7, **17**. 44, **18**. 33, 34, **27**. 42, **28**. 11, 12, 22. (in **28**. 12 behalve op Calluna ook op Vaccinium Myrtillus, ex. in herb. Kloos), C. europaea M8. **21**. 34, **31**. 12, Cynosurus cristatus 11 × in M7, 2 × in M8.

Dactylis glomerata 26 × in M7, 3 × in M8, Daucus Carota M7. **17**. 42, **28**. 12, 13, 23, 31, **38**. 12, 14, 23, M8. **31**. 11, Dianthus deltoïdes M7. **38**. 12, 14, 23 (hier ook heel licht), 24, M8. **21**. 34, **31**. 12, 13, Draba verna (= Erophila verna) wel bij vroegere invent., Drosera intermedia M7. **17**. 42, **28**. 21, 22, **37**. 41, **38**. 23, D. rotundifolia M7. **17**. 42, **18**. 44, **28**. 14, 21, 22, **37**. 41, **38**. 23,

Elodea canadensis M7. **28**. 24, 42, 44, M8. **31**. 12, Epilobium angustifolium 34 × in M7, 1 × in M8, E. hirsutum M7. **27**. 44, **28**. 24, 31, 33, 41, **37**. 23, **38**. 21, 23, 24, M8. **31**. 12, 13, E. montanum 11 × in M7, 1 × in M8, E. palustre 12 × in M7, 1 × in M8, E. parviflorum 10 × in M7, 2 × in M8, E. roseum 7 × in M7, 2 × in M8, E. tetragonum wel bij vroegere invent., E. virgatum (= obscurum) 22 × in M7, E. palustre × virgatum (= × E. Schmidtianum Rostk.) (nieuw) M7. **17**. 42, (ex. in herb. Kern & Reichgelt), E. roseum × virgatum (= × E. brachiatum Celak.) (nieuw) M7. **28**. 14, (ex. in herb. Kern & Reichgelt), Epipactis latifolia (= E. Helleborine) M7. **28**. 44, **38**. 14, 23, 24, 31, 32, M8. **31**. 12, Equisetum arvense 20 × in M7, 3 × in M8, E. limosum (= fluviatile) M7. **17**. 42, **28**. 12, 14, **37**. 23, **38**. 22, 24, M8. **21**. 34, **31**. 13, E. litorale (= E. arvense × limosum) (nieuw) M7. **27**. 44, **28**. 14, 24, 31, 33, 41, 43, 44, **37**. 23, **38**. 24, E. palustre 18 × in M7, 4 × in M8, E. silvaticum M7. **28**. 34 (ex. in herb. Kloos), Erica Tetralix 39 × in M7, 3 × in M8, E. T. flor. alb. (nieuw) M7. **37**. 22, Erigeron acer M7. **38**. 14, 23, M8. **31**. 12, E. canadensis 8 × in M7, 2 × in M8, Eriophorum polystachyum (= E. angustifolium) 12 × in M7, E. vaginatum wel bij vroegere invent., Erodium cicutarium f. pimpinellifolium 9 × in M7, Erysimum cheiranthoïdes M7. **28**. 31, 32, 42, M8. **21**. 34, **31**. 12, Erythraea Centaurium (= Centaurium umbellatum) M7. **38**. 23, M8. **31**. 12, Eupatorium cannabinum 21 × in M7, 4 × in M8, Euphorbia Cyparissias (nieuw) M7. **38**. 23, 24, E. Helioscopia M7. **28**. 12, 14, 21, 31, 32, 41, E. Peplus (nieuw) M7. **28**. 23, 32, Euphrasia Odontites (nieuw) M7. **37**. 24, E. officinalis-gracilis (nieuw) M7. **17**. 44, **28**. 22, E.o. - nemorosa 10 × in M7, 2 × in M8, E.o. - stricta 13 × in M7, 2 × in M8, Evonymus europaeus M7. **28**. 44, **38**. 22, 24, Fagus silvatica M7. **17**. 43, **28**. 11, 23, 32, Festuca arundinacea M7. **28**. 12, 13, 24, **38**. 12, 23, F. elatior (= F. pratensis) 17 × in M7, 2 × in M8, F. gigantea 9 × in M7, 1 × in M8, F. loliacea (= F. pratensis × Lolium perenne) in M7. **28**. 32 op dezelfde plek waar P. Jansen voor ± 20 jaar de plant al gevonden had, F. ovina, 23 × in M7, 3 × in M8, F. rubra 23 × in M7, 4 × in M8, Ficaria verna (= Ranunculus Ficaria) wel bij vroegere invent., Filago minima M7. **38**. 23, 24, M8. **31**. 13, Fragaria vesca 8 × in M7, F. v. fruct. alb. (nieuw) M7. **38**, 31, Fraxinus excelsior 18 × in M7, 1 × in M8, Fumaria officinalis M7. **28**. 32.

Galeobdolon luteum (= Lamium Galeobdolon) M7. **27**. 44, **28**. 31, 33, Galeopsis bifida 15 × in M7, 3 × in M8, G. ochroleuca (= G. segetum) M7. **17**. 44, **18**. 32, **28**. 13, 32, **38**. 23, 24, M8. **31**. 13, G. Tetrahit 36 × in M7, 3 × in M8, Galinsoga parviflora (nieuw) M7. **28**. 12, 31, 32, 41, G. quadriradiata (nieuw) M7. **45**. 11, d.i. bij station Almelo, M7. **28**. 31, ex. in herb. v. Ooststroom, Galium Aparine 20 × in M7, 3 × in M8, G. Mollugo 26 × in M7, 4 × in M8, G. palustre. 17 × in M7, 1 × in M8, G. saxatile M7. **28**. 11, 23, G. uliginosum 13 × in M7, 2 × in M8, G. verum M8. **21**. 34, Genista anglica 28 × in M7, 1 × in M8, G. pilosa M7. **17**. 42, **28**. 11, 23, **37**. 22, Gentiana Pneumonanthe 15 × in M7, Geranium dissectum (nieuw) M7. **28**. 32, 34, 41, G. molle M7. **27**. 44, **28**. 23, 32, **38**. 14, G. pusillum M7. **28**. 31, 32, G. Robertianum 15 × in M7, Geum urbanum 16 × in M7, 1 × in M8, Glechoma hederacea 20 × in M7, 2 × in M8, Glyceria fluitans 21 × in M7, 3 × in M8, G. plicata M7. **28**, 14, 34, 44, **38**. 12, 24, G. spectabilis (= G. maxima) 16 × in M7, 4 × in M8; ex. in herb. P. Jansen, Gnaphalium silvaticum M7. **17**. 42, 44, **18**. 34, **27**. 22, 42, **37**. 22, G. uliginosum 28 × in M7, 2 × in M8.

Hedera Helix 25 × in M7, 2 × in M8, Heleocharis acicularis (= Eleocharis acicularis, nieuw) M7. **28**. 44, Heleocharis palustris (= Eleocharis palustris) M7. **28**. 12, **38**. 32, Heleocharis uniglumis (= Eleocharis uniglumis, nieuw) M7, **28**. 22, Heleosciadium inundatum (= Apium inundatum) wel bij vroegere invent., Heracleum Sphondylium 21 × in M7, 2 × in M8, Hieracium Auricula M7, **27**. 44, **28**. 21, 22, 33, 44, H. laevigatum 18 × in M7, H. murorum M7. **28**. 34, 43, H. Pilosella 33 × M7, 4 × in M8, H. Sabaudum (nieuw) M7. **17**. 43, **27**. 24, **28**. 34, 43, H. umbellatum 25 × in M7, 3 × in M8, H. vulgatum (= H. Lachenalii) M7. **17**. 43, **18**. 43, **27**. 21, **28**. 12, 41, 43, Holcus lanatus 34 × in M7, 4 × in M8, H. mollis 22 × in M7, Hordeum murinum M7. **28**. 31, Hottonia palustris M7. **28**. 24, 42, **38**. 22, Humulus Lupulus 22 × in M7, 3 × in M8, Hydrocharis Morsus-ranae M7. **28**. 44, **38**. 24, M8. **31**. 11, 13, Hydrocotyle vulgaris 21 × in M7, 2 × in M8, Hypericum Helodes (= H. elodes) M7. **37**. 41, H. humifusum M7. **17**. 44, **28**. 11, H. perforatum 27 × in M7, 2 × in M8, H. quadrangulum (= H. maculatum) M7. **28**. 13, 42, M8. **21**. 24, **31**. 12, H. tetrapterum 16 × in M7, 1 × in M8, Hypochoeris radicata 21 × in M7, 1 × in M8.

Ilex Aquifolium 14 × in M7, Illecebrum verticillatum M7. **18**. 44, **27**. 21, **28**. 11, **37**. 22, **38**. 13, Impatiens Noli-tangere M7. **27**. 22, **28**. 23, 24, Iris Pseudacorus 13 × in M7, 1 × in M8.

Jasione montana 26 × in M7, 2 × in M8, Juncus bufonius 30 × in M7, 3 × in M8, J. compressus M7. **28**. 41, J. conglomeratus 32 × in M7, 3 × in M8, J. effusus 39 × in M7, 3 × in M8, J. effusus v. compactus (nieuw) M7. **17**. 43, **28**. 14, J. filiformis M7. **28**. 13, J. lamprocarpus (= J. articulatus) 17 × in M7, 1 × in M8, J. squarrosus 14 × in M7, J. supinus (= J. bulbosus) 8 × in M7, J. sylvaticus (= J. acutiflorus) 30 × in M7, 2 × in M8, Juncus tenageia M7. **28**. 11, J. tenuis (= J. macer) 35 × in M7, 3 × in M8, Juniperis communis 20 × in M7, 1 × in M8.

Lactuca muralis (= Mycelis muralis, nieuw) M7. **38**. 32, Lamium album 14 × in M7, L. amplexicaule M7. **28**. 32, L. purpureum M7. **18**. 32, **28**. 23, 32, 34, 43, M8. **31**. 12, Lampsana communis (= Lapsana communis) 21 × in M7, 1 × in M8, Lappa notha (= Arctium nothum, nieuw) M7. **27**. 22, 24, 44, **28**. 14, 23, 32, Larix decidua M7. **28**. 12, Lathyrus pratensis M7. **27**. 44, **28**. 32, 33, 34, 41, 43, Leersia oryzoides (nieuw) M7. **27**. 21, **38**. 24, 32, (ex. in herb. Kern & Reichgelt), Lemna minor 13 × in M7, 2 × in M8, L. polyrrhiza (= Spirodela polyrrhiza) M7. **17**. 42, **28**. 24, 34, M8. **31**. 12, Leontodon autumnalis 41 × in M7, 2 × in M8, Limnanthemum nymphaeoides (= Nymphoides peltata) M7. **37**. 41, 42, **38**. 14, 31, 32, Linaria vulgaris 9 × in M7, 4 × in M8, Linum catharticum M7. **38**. 23, Listera ovata wel bij vroegere inv., Littorella lacutris wel bij vroegere inv., Lobelia Dortmanna wel bij vroegere inv., Lolium multiflorum 13 × in M7, 2 × in M8, L. perenne 35 × in M7, 3 × in M8, Lonicera Periclymenum 31 × in M7, Lotus corniculatus M7. **17**. 42, **28**. 32, 34, **37**. 23, 24, M8. **21**. 34, L. uliginosus 34 × in M7, 3 × in M8, Lupinus luteus (nieuw) M7. **17**. 42, **27**. 42, **38**. 12, L. polyphyllus (nieuw) M8. **31**. 12, Luzula campestris 7 × in M7, 1 × in M8, L. multiflora 12 × in M7, 1 × in M8, L. multiflora v. congesta M7. **28**. 11, L. pilosa M7. **28**. 31, 32, Lychnis diurna (= Melandrium diurnum) M7. **17**. 43, **27**. 21, **37**. 31, **38**. 23, Lychnis Flos-cuculi 31 × in M7, Lychnis vespertina (= Melandrium album) M7. **28**. 31, Lychnis diurna × vespertina (= M. dubium, nieuw) M7. **28**. 31, Lycopodium clavatum M7. **28**. 23; ex. in herb. Kloos, L. inundatum M7. **17**. 42, **28**. 14, 22, **38**. 23, Lycopsis arvensis (nieuw) M7. **28**. 32, Lycopus europaeus 34 × in M7, 1 × in M8, Lysimachia nemorum M7. **28**. 24, **38**. 32, L. Nummularia 16 × in M7, 1 × in M8, L. thyrsiflora M7. **28**. 12, 24, 42, **38**. 32, L. vulgaris 30 × in M7, 4 × in M8, L. vulgaris Klinggraeffii M7. **28**. 31, Lythrum Salicaria 26 × in M7, 3 × in M8.

Maianthemum bifolium M7. **28**. 44, **38**. 24, 32, M8. **31**. 12, Malachium aquaticum M7. **28**. 32, 41, 42, 43, **38**. 24, M8. **31**. 13, Malva rotundifolia (= M. pusilla, nieuw) M7. **28**. 32, M. silvestris M7. **28**. 14, Matricaria Chamomilla 16 × in M7, 1 × in M8, M. discoidea (= M. matricarioides, nieuw) 18 × in M7, 2 × in M8, Medicago lupulina M7. **27**. 22, **28**. 13, 32, **38**. 12, 14, Melampyrum pratense 16 × in M7, 1 × in M8, Mentha aquatica 18 × in M7, 1 × in M8, M. arvensis 22 × in M7, M. velutina (nieuw) M7. **18**. 34, M. verticillata (nieuw) 11 × in M7, Menyanthes trifoliata M7. **17**. 42, **27**. 44, **28**. 22, 24, 33, 42, Milium effusum wel bij vroegere inv., Moehringia trinervia Mu. **17**. 42, **28**. 12, 23, 32, 41, **38**. 22, 24, Molinia coerulea 39 × in M7, 1 × in M8, Montia lamprosperma M7. **17**. 42, **18**. 33, **28**. 11, 12, 14, 21 (ex. in herb. Kloos, oudere ex., aanwezig in Rijksherb. en verenigingsherb., verzameld o.a. in 1905 als M. minor en als M. rivularis, bleken ook tot M. lamprosperma te behoren). Myosotis caespitosa M7. **17**. 43, **28**. 12, 43, **38**. 22, M8, **31**. 12, M. hispida (= M. collina) M7. **28**. 12, M. intermedia (= M. arvensis) 15 × in M7, M. palustris (= M. scorpioïdes) 22 × in M7, 2 × in M 8, M. versicolor M7. **38**. 22, 32, Myrica Gale 17 × in M7, 1 × in M8, Myriophyllum spicatum M7. **37**. 42, **38**. 14, 23, 24, 32.

Nardus stricta 20 × in M7, 2 × in M8, Narthecium ossifragum M7. **17**. 42, **28**. 21, 22, **38**. 23, Nasturtium amphibium (= Rorippa amphibia) M7. **28**. 14, 24, 42, 44, **38**. 21, M8. **21**. 34, Nasturtium officinale M7. **17**. 42, 38. 24, 42, **38**. 32, N. palustre (= Rorippa islandica) M7. **27**. 22, **28**. 11, 12, 21, 34, **38**. 21, 22, M8. **31**. 12, N. silvestris (= Rorippa silvestris) M7. **28**.

12, Nuphar luteum 10 × in M7, 3 × in M8, Nymphaea alba 9 × in M7, 3 × in M8.

Oenanthe fistulosa 12 × in M7, 1 × in M8, Oe. Phellandrium (= Oe. aquatica) M7. **28**. 42, 44, **38**. 21, 22, 24, M8. **31**. 11, 12, Oenothera biennis M7. **28**. 23, **38**. 24, M8. **21**. 34, Orchis incarnata wel bij vroegere inv., O. latifolia M7. **17**. 42, O. maculata M7. **17**. 42, **27**. 42, **37**. 41, **38**. 23, Ornithogalum umbellatum wel bij vroegere inv., Ornithopus perpusillus 16 × in M7, 2 × in M8, O. sativus (nieuw) M7. **17**. 42, 43, 44, Osmunda regalis M7. **28**. 21, 42, **38**. 23, Oxalis Acetosella 9 × in M7, O. stricta M7. **27**. 44, **28**. 23, 32, 33, 34, 43, **38**. 11.

Panicum Crus-galli (= Echinochloa Crus-galli) 21 × in M7, Panicum lineare (= Digitaria Ischaemum) 8 × in M7, 2 × in M8, Papaver dubium M7. **28**. 32, P. somniferum (nieuw) M7. **28**. 12, 32, 42, Paris quadrifolia M7. **38**. 14, 32, Parnassia palustris M7, **17**. 42, **38**. 14, 32, Pastinaca sativa (nieuw) M8. **21**. 34, **31**. 12, Pedicularis palustris wel bij vroegere inv., P. sylvatica M7. **17**. 42, 43, **28**. 11, 22, 44, Peplis Portula M7. **17**. 44, **18**. 44, **28**. 12, 14, 22, 24, 44, **38**. 21, Petasites officinalis (= P. hybridus) M7. **28**. 23, 34, Phalaris arundinacea 17 × in M7, 2 × in M8, Phegopteris Dryopteris (= Dryopteris Linnaeana) wel bij vroegere inv., Phleum pratense 11 × in M7, 1 × in M8, Phragmites communis 19 × in M7, 3 × in M8, Physalis Franchetii (nieuw) M7. **28**. 34, Pilularia globulifera wel bij vroegere inv., Pimpinella saxifraga 12 × in M7, 3 × in M8, Pinguicula vulgaris M7. **17**. 42, Pinus silvestris 26 × in M7, Pirus communis wel bij vroegere inv., P. malus pumila M7. **27**. 22, 24, **28**. 31, Plantago lanceolata 42 × in M7, 4 × in M8, P. major 42 × in M7, 4 × in M8, Platanthera bifolia M7. **17**. 42, **18**. 33, **28**. 12/21, Poa annua 43 × in M7, 3 × in M8, P. nemoralis 9 × in M7, 1 × in M8, P. pratensis 17 × in M7, 3 × in M8, P. serotina (= P. palustris) M7, **27**. 21, 44, **28**. 24, 33, 44, **38**. 21, M8. **21**. 34, **31**. 12, P. trivialis 13 × in M7, Polygala depressa (= P. serpyllifolia, nieuw) M7. **18**. 33, **28**. 12/21, P. vulgaris M7. **18**. 33, **28**. 12/21, **38**. 23, Polygonatum multiflorum M7. **28**. 31, **38**. 14, 32, M8. **31**. 12, Polygonum amphibium 19 × in M7, 3 × in M8, P. aviculare 33 × in M7, 4 × in M8, P. Convolvulus 19 × in M7, 2 × in M8, P. cuspidatum (nieuw) M7. **28**. 32, P. dumetorum 11 × in M7, 4 × in M8, P. Fagopyrum (= Fagopyrum sagittatum) M7. **17**. 44, **27**. 44, **28**. 33, P. Hydropiper 25 × in M7, P. lapathifolium 22 × in M7, 2 × in M8, P. minus (nieuw) 11 × in M7, 1 × in M8, P. mite 14 × in M7, P. nodosum M7. **27**. 42, **28**. 13, 21, 31, 41,44, P. Persicaria 22 × in M7, 1 × in M8, P. tataricum (= Fagopyrum tataricum, nieuw) M7. **17**. 44, **27**. 44, Polypodium vulgare 21 × in M7, Polystichum Filix-mas (= Dryopteris Filix-mas) 20 × in M7, 2 × in M8, P. spinulosum (= D. austriaca) 27 × in M7, waarvan 19 × ssp. dilatatum en 12 × ssp. eu-spinulosum, Populus canadensis M7, **37**. 23, 24, 41, P. canescens (nieuw) M7. **28**. 11, P. nigra (nieuw) M7. **28**. 32. P. serotina M7. **28**. 11, P. tremula 25 × in M7, 1 × in M8, Potamogeton crispus (nieuw) M7. **28**. 34, **37**. 41, 42, P. lucens M7. **38**. 14, 23, 24, 32, M8. **31**. 12, 13, P. natans M7. **28**. 12, 24, 42, 44, P. pectinatus (nieuw) M7. **38**. 14, 24, 32, P. perfoliatus M7. **37**. 41, 42, **38**. 14, 23, 24, 32, M8. **31**. 12, 13 P. polygonifolius (= P. oblongus) M7. **28**. 14, Potentilla Anserina 23 × in M7, 4 × in M8, P. reptans (nieuw) M7. **28**. 41, P. Tormentilla (= P. erecta) 41 × in M7, 3 × in M8, Primula elatior M7. **38**. 14, Prunella vulgaris 35 × in M7, 3 × in M8, P. v. fl.alb. M7. **28**. 13, P. v. fl.roseis M7. **28**. 12, 22, 31, 43, **38**. 14, Prunus avium M7. **17**. 42, **28**. 14, 23, 41, 44, **38**. 24, P. domestica wel bij vroegere inv., P. Padus 10 × in M7, 1 × in M8, P. serotina M7. **17**.

44, **28**. 11, 42, P. spinosa. 19 × in M7, Pteris aquilina (= Pteridium aquilinum) 14 × in M7, 1 × in M8, Pulicaria dysenterica M8. **31**. 12.

Quercus Robur 45 × in M7, 2 × in M8, Q. rubra M7. **18**. 34, **28**. 31, 44, **38**. 24.

Radiola Linoïdes M7. **28**. 22, Ranunculus acer 32 × in M7, 3 × in M8, R. auricomus wel bij vroegere inv., R. Flammula 23 × in M7, 1 × in M8, R. Lingua M8. **31**. 13, R. repens 34 × in M7, 3 × in M8, R. sceleratus M7 in **28**. 31, 34, 41, 42, Raphanus Raphanistrum (nieuw) M7. **17**. 43, **27**. 44, **28**. 13, 23, 31, 33, Rhamnus catharticus M7. **38**. 32, Rh. Frangula (= Frangula Alnus) 41 × in M7, 1 × in M8, Rhinanthus major (= Rh. glaber) 26 × in M7, 3 × in M8, vaak in ssp. montanus Schwartz, Rh. minor (nieuw) M7. **28**. 41, Rhynchospora alba M7. **17**. 42, **28**. 21, **37**. 41, **38**. 23, Rh. fusca M7. **17**. 42, **28**. 21, **37**. 41, **38**. 23, Ribes Grossularia (= R. Uva-crispa) M7. **28**. 12. R. nigrum M7. **28**. 23, 24, 42, 43, 44, **38**. 24, R. rubrum (= R. silvestre) M7. **27**. 22, **28**. 44, Robinia Pseudo-Acacia 8 × in M7, Rosa canina 17 × in M7, 1 × in M8, R. dumetorum (nieuw) 7 × in M7, 2 × in M8, R. rugosa M7. **28**. 42, Rubus caesius M7. **28**. 24, **38**. 32, M8. **31**. 12, R. idaeus 23 × in M7. 2 × in M8, R. plicatus (nieuw) M7. **17**. 42, **28**. 12, 23, R. suberectus (nieuw) M7. **17**. 43, **27**. 22, **28**. 14, 23, 31, 43, **38**. 21, R. div. spp. 38 × in M7, Rumex Acetosa 32 × in M7, 4 × in M8, R. Acetosella 36 × in M7, 3 × in M8, R. acutus (= R. pratensis, nieuw) M7. **28**. 31, R. conglomeratus 17 × in M7, 3 × in M8, R. crispus M7. **28**. 24, 31, 32, 34, 44, M8. **21**. 34, **31**. 12, R. Hydrolapathum 15 × in M7, 4 × in M8, R. obtusifolius 24 × in M7, 1 × in M8, R. sanguineus M7. **27**. 44, **28**. 24, 34, 41, **38**. 21. 24.

Sagina nodosa (nieuw) M7. **38**. 14, 23, M8. **31**. 12, 13, S. procumbens 14 × in M7, 1 × in M8, Sagittaria sagittifolia M7. **28**. 24, 44, **37**. 42, **38**. 23, M8 **21**. 34, **31**. 11, 12, Salix alba 11 × in M7, 1 × in M8, S. amygdalina (= S. triandra, nieuw) M7. **28**. 11, 24, 34, 41, 44, **38**. 24, M8. **21**. 34, **31**. 12, S. aurita 30 × in M7, S. Caprea × 9 in M7, S. cinerea 28 × in M7, 1 × in M8, S. purpurea (nieuw) M7. **28**. 41, S. repens 30 × in M7, 2 × in M8, S. undulata (= S. alba × triandra, nieuw) M7. **28**. 34, S. viminalis M7. **18** 44, **28**. 12, 14, 31, 42, **38**. 24, M8. **21**. 34, S. aurita × cinerea (nieuw) M7. **28**. 14, 44, S. Caprea × cinerea (nieuw) M7. **28**. 34, S. cinerea × viminalis. (nieuw) M7. **28**. 13, Sambucus nigra 10 × in M7, Sanicula europaea M7 **38**. 14, 32, Sarothamnus scoparius 37 × in M7, 4 × in M8, Scirpus caespitosus (= Trichophorum caespitosum) M7. **17**. 42, **28**. 11, 14, **37**. 41, **38**. 23; alleen ssp. germanicus (Palla), Scirpus fluitans (= Isolepis fluitans) wel bij vroegere inv., Scirpus lacustris (= Schoenoplectus lacustris) M7. **28**. 24, **38**. 31, 32, Scirpus pauciflorus (= Eleocharis pauciflora) M7, **17**. 42, Scirpus setaceus (= Isolepis setacea) M7. **17**. 42, **28**. 12, 22, 24, 42, Scirpus silvaticus 14 × in M7, 1 × in M8, Scleranthus annuus 19 × in M7, 3 × in M8, Scrophularia alata (Balbisii of Neesii?) M7. **28**. 42, S. nodosa 19 × in M7, 1 × in M8, Scutellaria galericulata 9 × in M7, 2 × in M8, Secale cereale (= Triticum cereale) M7. **17**. 43, 44, **18**. 34, **27**. 24, **28**. 12, 34, 41, Sedum purpureum (= S. Telephium ssp. purpureum) M7. **17**. 43, **28**. 31, 42, 44, **38**. 24, M8. **31**. 11, Sempervivum tectorum (nieuw) M7. **28**. 43, Senecio aquaticus 16 × in M7, 1 × in M8, S. Jacobaea (nieuw) M7. **38**. 23, S. silvaticus 23 × in M7, 1 × in M8, S. viscosus (nieuw) M7. **28**. 32, S. vulgaris 13 × in M7, Setaria glauca (= S. pumila, nieuw) M7. **28**, 12, S. viridis (nieuw) M7. **28**. 14, 32, Silene inflata (= S. vulgaris) M7. **38**. 14, M8. **31**. 13, Sinapis arvensis M7. **27**. 44, **28**. 33, 34, Sisymbrium officinale 16 × in M7, 3 × in M8, S. Thalianum (= Arabidopsis Thaliana) M7. **38**. 23, M8. **21**. 34, **31**. 12, Sium latifolium M7. **28**. 43, 44, **38**. 21, 23, 24, M8. **31**. 13, Solanum Dulcamara) 18 × in M7, 2 × in M8, S. D. flor. alb. M8, **21**. 34 (ex. in herb. Kloos, S. nigrum 12 × in M7, S. tuberosum M7. **17**. 43, **18**. 34, **27**. 42, **28**. 31, Solidago serotina (nieuw) M7. **17**. 43, **28**. 23, S. Virga-aurea M7. **17**. 43, **28**. 31, **38**. 22, 31, 32, M8, **31**. 12, Sonchus arvensis M7. **27**. 21, 42, 44, **28**. 12, S. asper 10 × in M7, 1 × in M8, S. oleraceus 8 × in M7, 1 × in M8, Sorbus Aucuparia 43 × in M7, 1 × in M8, Sparganium affine (= S. angustifolium) wel bij vroegere inv., S. minimum M8. **31**. 13, S. ramosum (= S. erectum) 17 × in M7, 1 × in M8, waarbij 7 × herkend de ssp. neglectum, S. simplex M7, **18**. 43, **28**. 12, **38**. 24, M8. **21**. 34, **31**. 12, 13, Spergula arvensis 30 × in M7, 3 × in M8, S. Morisonii (= S. vernalis) wel bij vroegere inv., Spergularia rubra M7. **17**. 43, 44, **28**. 12, 21, 32, **38**. 14, 23, 24, Spiraea salicifolia M7. **28**. 41, M8. **21**. 34, **31**. 11, S. Ulmaria (= Filipendula Ulmaria) 25 × in M7, 3 × in M8, Stachys arvensis M7. **28**. 31, 34, **38**. 22, S. palustris 23 × in M7, 3 × in M8, S. silvatica 24 × in M7, 1 × in M8, Stellaria glauca (= S. palustris) M7. **27**. 42, **28**. 23, 42, 44, **38**. 22, M8, **21**. 34, S. graminea 29 × in M7, 4 × in M8, S. Holostea 13 × in M7, 1 × in M8, S. media 27 × in M7, 1 × in M8, S. nemorum wel bij vroegere inv., S. uliginosa (= S. Alsine) 14 × in M7, 1 × in M8, Stratiotes aloïdes (nieuw) M7. **28**. 24, Succisa pratensis 34 × in M7, 3 × in M8, Symphytum officinale M7. **18**. 44, **28**. 21, 31, 34, 42, 43.

Tanacetum vulgare 30 × in M7, 4 × in M8, Taraxacum officinale 35 × in M7, 4 × in M8, Taxus baccata wel bij vroegere invent., Teesdalia nudicaulis 8 × in M7, Teucrium Scorodonia M7. **27**. 44, **28**. 31, 33, Thalictrum flavum M7. **28**. 24, **38**. 23, Thlaspi arvense wel bij vroegere invent., Thrincia hirta (= Leontodon nudicaulis) M7. **28**. 11, 12, 14, 23, 34, 41, 42, Thymus Serpyllum ssp. Chamaedrys (= Th. pulegioïdes) M7. **38**. 14, 23, 24, M8. **21**. 34, **31**. 11, 12 d.i. alle langs het kanaal Almelo-Nordhorn, Thysselinum palustre (= Peucedanum palustre) 13 × in M7, 2 × in M8, Tilia ulmifolia (= Tilia cordata) wel bij vroegere inv., Torilis Anthriscus (= T. japonica) 16 × in M7, 3 × in M8, Trifolium arvense M7. **38**. 12, 14, 23, 24, M8. **31**. 11, 13, T. hybridum 21 × in M7, T. incarnatum (nieuw) M7. **17**. 42, T. minus (= T. dubium) 21 × in M7, 2 × in M8, T. pratense 44 × in M7, 4 × in M8, T. p. fl. alb. M7, **28**. 34, T. repens 46 × in M7, 4 × in M8, T. r. flor. ros. M7. **28**. 41, Triglochin palustre M7. **17**. 42, **28**. 22, 42, **38**. 32, Triodia decumbens (= Sieglingia decumbens) 16 × in M7, 2 × in M8, Triticum repens (= Agropyrum repens) 9 × in M7, 2 × in M8, Tussilago Farfara 12 × in M7. 2 × in M8, Typha angustifolia in zeer fijnbladige vorm M7. **28**. 21, T. latifolia 9 × in M7, 1 × in M8.

Urtica dioica 34 × in M7, 3 × in M8, U. urens M7. **27**. 22, **28**. 32, 41, 43, **38**. 22, Utricularia minor (nieuw) M7. **17**. 42.

Vaccinium Myrtillus 24 × in M7, 3 × in M8, V. Oxycoccus (= Oxycoccus quadripetalus, nieuw) M7. **17**. 42, **38**. 23, V. Vitis-idaea 12 × in M7, 3 × in M8, Valeriana dioica 10 × in M7, V. officinalis 29 × in M7, 1 × in M8, Valerianella olitoria (= V. Locusta) wel bij vroegere inv., Verbascum nigrum (nieuw) M7. **28**. 13, V. Schraderi (= V. Thapsus, nieuw) M7. **28**. 14, Veronica agrestis M7. **17**. 43, **28**. 32, V. Anagallis M7. **28**. 34, **38**. 12, V. arvensis M7. **28**. 12, 13, 21, 31, 34, 41, M8. **31**. 12, V. Beccabunga M7. **28**. 23, 24, 32, 42, **38**. 12, 21, V. Chamaedrys 9 × in M7, 1 × in M8, V. hederaefolia wel bij vroegere inv., V. longifolia M8. **21**. 34, **31**. 12, V. officinalis M7. **28**. 12, 31/32, 43, **38**. 32, V. scutellata M7. **17**. 42, **28**. 11, 12, **38**. 21, V. serpyllifolia M7. **17**. 42, **28**. 31, 44, **37**. 22, **38**. 14, 23, 24, Viburnum Opulus 13 × in M7, 1 × in M8, Vicia angustifolia 19 × in M7, V. Cracca 25 × in M7, 2 × in M8, V. hirsuta 10 × in M7, 1 × in M8, V. sepium wel bij vroegere inv., V. villosa wel bij vroegere inv., Viola canina M7. **28**. 12, 23, 44, **37**. 42, **38**. 23, M8. **21**. 34, **31**. 12, V. palustris 14 × in M7, 1 × in M8, V. Riviniana 11 × in M7, 1 × in M8, V. silvestris nog wel bij vroegere inv. genoteerd, V. canina × Riviniana (nieuw) M7. **17**. 44, V. tricolor ssp. arvensis 19 × in M7, V. tricolor ssp. vulgaris M7. **17**. 44, **28**. 42, **37**. 23.

Jan G. Sloff.

VERSLAG van de Subcommissie voor het Zuiderzee-onderzoek over het jaar 1946.

Op het punt van verschijnen staat Mededeling No. 47 door P. Jansen: Het werk der Zuiderzeecommissie. Het Correspondentieblad verscheen eenmaal, waarmee deel VI werd afgesloten.

De volgende excursies werden gehouden: Oostrand van het IJsselmeer door Kloos, Kruseman en Vlieger (Juni), kust tussen Elburg en Harderwijk (van April tot October), Noordoostpolder door Boer en Feekes (regelmatig, in September met P. Jansen en Kloos); Zeeburg — Diemerdam door Kruseman en Piet (September); Durgerdam door Croockewit en Kruseman (Juni).

Het secretariaat ging aan het einde van het jaar over van J. L. van Soest naar H. W. E. Croockewit.

De Secretaris,
J. L. van Soest.

VERSLAG van de Commissie voor de Biosociologie en het Veenonderzoek in Nederland over 1946.

Op 27 Januari werd Prof. Dr A. A. Pulle als voorzitter van de Commissie vervangen door Dr A. Scheygrond.

De reisgelegenheid was dit jaar weer zover hersteld, dat deze geen belemmering meer vormde voor het bijwonen der „Sociologendagen”. Er zijn in 1946 twee „Sociologendagen” gehouden en wel op 26 Mei en op 15 December.

De 17e Nederlandse Dag voor Biosociologie en Palaeobotanie werd door 45 deelnemers bijgewoond. Er werden voordrachten gehouden door Dr E. C. Wassink, Mr F. Florschütz, Dr D. M. de Vries en Dr F. P. Jonker. De aangekondigde voordrachten van V. Westhoff en Th. A. de Boer vervielen, resp. door drukke bezigheden in verband met promotie en wegens bezwaren tegen de Zondag als vergaderdag. Er was een levendige gedachtenwisseling over de verschillende onderwerpen.

De 18e „Sociologendag” was weer gekenmerkt door een ouderwets aantal deelnemers, nl. 79. Er werden voordrachten gehouden door M. F. Mörzer Bruyns, Dr L. G. Tinbergen, Dr E. M. van Zinderen Bakker, Ir G. Sissingh en J. van der Drift, welk programma vlot afgewerkt werd. Een voorstel van J. Meltzer werd aanvaard om na adhaesie van de Commissie tot Bescherming van de wilde Flora het Bestuur der Kon. Ned. Bot. Vereeniging te verzoeken een adres te richten aan de Ministers van Onderwijs, Kunsten en Wetenschappen en van Landbouw, Visserij en Voedselvoorziening teneinde aan te dringen op bescherming van een deel van het plantensociologisch belangrijke dal van de Beerze in Noord-Brabant.

Wageningen, 7 Februari 1947. Dr D. M. de Vries.

VERSLAG van de Zeventiende Nederlandse Dag voor Biosociologie en Palaeobotanie, gehouden op 26 Mei 1946 in de Collegezaal van het Botanisch Laboratorium te Utrecht.

Na de opening door de voorzitter, Dr A. Scheygrond, sprak eerst Dr E. C. Wassink over:

Enkele sociologische en plantengeografische opmerkingen in verband met de hoogveenvegetatie der Engbertsdijkvenen bij Vriezenveen.

Er zijn 3 redenen om, na de bespreking van deze vegetatie op de 5e sociologendag [14-11-'37, Ned. Kruidk. Archief **48**, 51 (1938)] hierop nog eens terug te komen, nl.:

1. Er werden door F. Florschütz en spr. sindsdien vele aanvullende waarnemingen over de vegetatie gedaan.
2. Er verschenen in de omliggende landen beschrijvingen van hoogveenvegetaties, waaruit blijkt, dat het genoemde Nederlandse hoogveen hierin goed past.

   Uiteraard wordt hierdoor het belang van reservering van een karakteristiek deel van dit terrein voor ons land vergroot, terwijl helaas geconstateerd moet worden, dat ondanks de in 1937 vanuit deze vergadering gegeven aanbeveling in deze richting nog niets daadwerkelijks tot stand is gekomen.

Aan de hand van vegetatieschetsen en foto's werd nogmaals een korte beschrijving van het terrein gegeven. Het blijkt, dat de successie ongeveer als volgt moet worden gedacht: Zwarte naakte slenken met enkele planten van *Rhynchospora alba*, *Sphagnum cuspidatum*, *Drosera intermedia* en *Eriophorum polystachyon*, in natte perioden met water bedekt (zone 1), gaan over in een begroeiing van *Rhynchospora alba* met *Spaghnum cuspidatum*, met *Drosera intermedia* en *Eriophorum polystachyon* (zone 2); op de iets hogere plekken vindt men grofbladige Sphagna [in 't bizonder *Sph. magellanicum* (= *Sph. medium*) en *Sph. papillosum*] en ook *Erica Tetralix* (zone 3). Hierin vindt men verder: *Drosera rotundifolia, Andromeda*, echter geen *Drosera intermedia*. Nog hoger vindt men een *Ericetum* met grofbladige Sphagna, *Leucobryum*-bulten, pollen van *Scirpus caespitosus* en ook *Calluna* (zone 4). Op de hoogste plekken eindelijk wordt een *Calluna-Cladonia*-vegetatie aangetroffen met *Erica, Molinia*, levermossen en gedegenereerde Sphagna (zone 5). In enkele gevallen wees de gevonden situatie erop, dat plekken van de zone 3 een klein areaal van de zone 5 omringen, er bovenuit groeien en de hei tot afsterving brengen, waardoor een kale plek (zone 1) ontstaat. De sedert 1937 gedane waarnemingen en vegetatieopnamen steunen dit, in grote trekken reeds destijds gevormde beeld. Het blijkt, dat de door TÜXEN (1937) voor de hoogveenvegetatie onderscheiden associaties voor een sociologische beschrijving van de vegetatie der Engbertsdijkvenen een alleszins bruikbare grondslag vormen. Zo vertoont de zone 2 duidelijke trekken van overeenkomst met *Scheuchzerion*-associaties, in 't bijzonder met het *Scheuchzerietum palustris* TX. 1937, in fragmentaire ontwikkeling, zonder de zeer zeldzame karaktersoorten, waarop, behalve de soortencombinatie, het ontbreken van *Rhynchospora fusca* schijnt te wijzen. Zone 3 komt goed overeen met het *Sphagnetum medii subatlanticum typicum* TX. 1937, zone 4 met het *Ericetum tetralicis sphagnetosum* ALLORGE 1926. Zone 5 is misschien op te vatten als een soortenarm fragment van het *Calluneto-Genistetum molinietosum* TX. 1937. Hoewel door de mozaïekvormige wisseling der gezelschappen op beperkt terrein de associaties topografisch niet scherp gescheiden zijn, komt het ons voor, dat door TÜXEN de ontwikkelingsphasen der hoogveenvegetatie treffend zijn gekarakteriseerd.

Bij vergelijking met beschrijvingen van andere hoogvenen blijkt, dat in het Deense „Store Vildmose" door JESSEN verschillende ontwikkelingsreeksen zijn beschreven, waarvan een doet denken aan bepaalde successies in Komosse volgens OSVALD, een andere met *Eriophorum polystachyon* en *Erica* aan de in Vriezenveen gevondene. Door JONAS werden uit het Papenburgerveen eveneens vegetaties en successies beschreven, welke met die van Vriezenveen verwantschap vertonen. Tenslotte beschreven GODWIN en CONWAY een veen in Wales, waarin wij eveneens dezelfde elementen terugvinden, zowel in details van de successie als in het algemene beeld van de vegetatie. Ook deze auteurs vermelden, dat degeneratiestadia (de sluitsteen der successie) moeilijk te vinden zijn, evenals zulks in Vriezenveen het geval is.

Alles bij elkaar past het te Vriezenveen aanwezige vegetatiebeeld goed in wat in de wijdere omgeving is gevonden. Het is te hopen, dat het nog lukt althans iets van dit in ons land geheel enige en opmerkelijke begroeiingstype te behouden. Een uitvoeriger beschrijving zal binnenkort worden gepubliceerd.

De tweede spreker was Mr F. FLORSCHÜTZ, met een mededeling, getiteld:

Poging tot ouderdomsbenadering van de Gelderse löss langs geologisch-palynologische weg.

Weinigen uwer zullen het heuvellandschap niet kennen, dat zich tussen Velp en Dieren ten noorden van de Rijksweg ter breedte van enkele kilometers uitstrekt en dat o.a. de bossen van Beekhuizen, Heuven en Hagenau draagt. Het is bedekt met een stoffijne grondsoort, waarop de beuk zich goed thuis voelt: de „boekegrond”. In een van die bossen groeit als merkwaardigste plant *Trientalis europaea* en buiten het bos vindt men er het grootste complex Gaspeldoorn in ons land. Opvallend zijn, ook op de heuvels, de grote uitgestrektheden *Erica*, waartussen rijkelijk *Lycopodium clavatum* en onder de Korstmossen de zeldzame *Baeomyces placophyllus*, die ik echter in de laatste jaren niet heb kunnen terugvinden.

De landbouw trekt profijt van de goede eigenschappen van de grond: de boer verbouwt zijn rogge, haver en aardappelen ook op de hellingen, zoals zijn Zuidlimburgse collega dat doet.

Ook door de holle wegen, typisch voor een lössgebied, vertoont het landschap enige gelijkenis met Zuid-Limburg.

Volgens het recente proefschrift van VAN DOORMAAL is löss in geologische zin „het sedimentgesteente met karakteristiek korrelgrootte-maximum van 85 tot 60% tussen 0.05 en 0.01 mm en een karakteristieke mineraalassociatie, waarvan de afzetting te danken is aan de wind gedurende een glaciale periode”.

Wat de korrelgrootte betreft, mogen we het materiaal van de Veluwezoom zeker löss noemen: Prof. HUDIG te Wageningen was zo vriendelijk het sediment op korrelgrootte te onderzoeken; hij vond, dat de z.g. aeolische fractie, dat zijn de korrels tussen 50 en 2μ, bijna 80% van het geheel bedroeg.

Over de mineralogische samenstelling van deze afzetting deelt EDELMAN mede, dat de overeenkomst met de Limburgse löss opvallend is. We zullen dus terecht van Gelderse löss mogen spreken.

De löss van de Veluwezoom ligt op zand met grint, dat de geologische kaart „gestuwd praeglaciaal” noemt. Dat is het door de grote rivieren in het eerste deel van de voorlaatste ijstijd, het Rissglaciaal, aangevoerd materiaal, dat in het tweede deel van die ijstijd door de gletschers tot een stuwmoraine vervormd werd. Toch heeft dit heuvellandschap niet door het ijs van de Riss en evenmin door smeltwaterwerking zijn tegenwoordig relief verkregen. Dat moet later zijn gebeurd, want er bestaan belangrijke morphologische verschillen tussen de terreinen, die door de gletschers van de laatste ijstijd, het Würmglaciaal, bedekt waren, en de westelijk daarvan gelegene, die toen niet, maar vroeger wel vergletscherd waren. Dit is gebleken bij vergelijking van jong-glaciale landschappen ten oosten van de Elbe met westelijker oud-glaciale. Vooral Gripp heeft op die verschillen de aandacht gevestigd. Het oudere moraine landschap onderscheidt zich van het jongere, voornamelijk doordat het eerste talrijke, radiair geordende, droge dalen vertoont. Aan de Veluwezoom is dat van de Zijpenberg af goed te zien.

Dat verschil kan niet anders verklaard worden dan door periglaciale erosie in het Würmglaciaal. Buiten het vergletscherde gebied was de bodem voortdurend bevroren en alleen in de zomer ontdooide hij oppervlakkig. Het eigenlijke grondwater stond heel laag, maar de bevroren ondergrond verhinderde het wegzakken van het regen- en smeltwater, zodat dit bij het weinig gesloten toendraplantendek sterk eroderend kon werken; alleen grintlagen konden aan die erosie weerstand bieden. Ook de krachtige winden droegen tot de erosie bij. Het resultaat was, dat diepe dalen uitgeslepen werden tussen de harde grintkoppen.

Dat beeld biedt de Veluwezoom nu. De erosie is thans zwak; het regenwater zakt snel weg en de dalen liggen op een enkel na droog.

Over dit erosielandschap ligt het lössdek uitgespreid als een kleed, zelden dikker dan 2 m. Alleen de harde grintkoppen steken er boven uit, als gaten in dat kleed.

Hoe oud is dat dek? Het werd na de erosie gelegd en kan dus niet ouder zijn dan de Würmijstijd, zelfs niet ouder dan het laatste stadium daarvan. Was het ouder, dan zou het door de erosie in dat laatste stadium weer verdwenen zijn. Waarnemingen in China bevestigen, dat de löss, overal waar ze niet vlak ligt, zeer vatbaar is voor erosie.

Door de onderzoekingen van Soergel is aangetoond, dat lösssedimentatie plaats vond bij de nadering en in het maximum van een ijstijd. Wat de Veluwezoom betreft, kan dit niet anders zijn geweest dan het laatste stadium van de laatste ijstijd. In Natura van Augustus 1940 kwam Edelman ook tot de conclusie, dat de löss van de Veluwezoom een jeugdige vorming moet zijn.

Directe ouderdomsbepaling van de löss zou mogelijk zijn, als dat sediment voldoende stuifmeelkorrels bevatte, afkomstig uit de tijd, waarin het gedeponeerd werd. We zouden dan de methode kunnen toepassen, die tot voor kort algemeen pollenanalyse werd genoemd.

Tegen dat woord kan het bezwaar worden ingebracht, dat het slechts ten dele weergeeft, wat de methode omvat, nl. de analyse van het pollen en niet van de sporen van varens, mossen, enz. Twee Engelsen, Hyde en Williams, uit Cardiff, Wales, hebben getracht, dat bezwaar te ondervangen door „pollenanalysis" te vervangen door „palynology", afgeleid van *παλύνω*, dat uitstrooien betekent. Dat omvat dus de kennis van alles, wat wordt uitgestrooid, pollen èn sporen.

Hyde en Williams stelden die vervanging voor in het Octobernummer 1944 van Pollen Analysis Circular, een in de oorlog in de Verenigde Staten opgericht tijdschrift, onder redactie van Prof. Sears te Oberlin, Ohio. Het nieuwe woord achten zij niet alleen juister, maar ook welluidend, terwijl als bijkomstig voordeel wordt beschouwd, dat het het woord „pollen" suggereert. Mij dunkt, dat het aanbeveling kan verdienen, hun raad te volgen.

In de löss van de Veluwezoom werden helaas geen pollenkorrels of sporen gevonden. Dat behoeft ons niet te verwonderen, want dat sediment is sterk geaereerd en tegen niets zijn stuifmeelkorrels en sporen zo slecht bestand als tegen zuurstof. Behandeling met salpeterzuur en fluorwaterstof verdragen zij, maar langdurige inwerking van de lucht niet.

Zou het gelukken, ergens löss te vinden, die voldoende van de lucht afgesloten was gebleven, dan bestond er een redelijke kans op palynologisch succes. Zodanige afsluiting kan door water worden verkregen. Gezocht moest worden naar löss, in water afgezet en later niet uitgedroogd. Löss onder veen zou aan die voorwaarde kunnen voldoen. Aan de Veluwezoom kon ik dit niet vinden, maar wel in een ander Gelders lössgebied, nl. dat tussen Ubbergen en de Plasmolen. Algemeen wordt aangenomen, dat die löss, wat herkomst en ouderdom betreft, gelijk is aan die van de Veluwezoom. Prof. Hudig vond, dat de aeolische fractie wisselde tussen 62 en 77%. Mineralogisch zijn mij nog geen gegevens bekend.

Bij Groesbeek geeft de geologische kaart moerasveen aan in het Bruuk. Bij een boring bleek, dat onder het veen ongeveer één meter sediment voorkwam met een aeolische fractie van 65%. In dat opzicht onderscheidt het zich dus niet van de onbedekte löss in de omgeving. Het gehalte aan allerfijnste partikeltjes, kleiner dan 2μ, het z.g. lutum, is echter groter. Daaruit mag worden afgeleid, dat de löss in het Bruuk door een moeras werd opgevangen. Hierop wijst ook de omstandigheid, dat bij de microanalyse de alg *Pedias-*

trum boryanum werd gevonden en radicellen van *Carex* werden aangetroffen. Voorts bleek deze löss koolzure kalk te bevatten, die ze elders mist, en voldoende stuifmeel voor analyse.

Onder de löss bij Groesbeek komt een keienvloer voor, die ook aan de Veluwezoom kon worden waargenomen. Dit is ook een bewijs van erosie vòòr de lössafzetting. Het zand werd op deze plaats weggeblazen, zodat een concentratie van stenen plaats vond. Neemt men in aanmerking, dat in het onderliggende zand stenen zeldzaam zijn, dan kan men zich voorstellen, dat veel zand weggeblazen moest worden, voordat de keienvloer gevormd was.

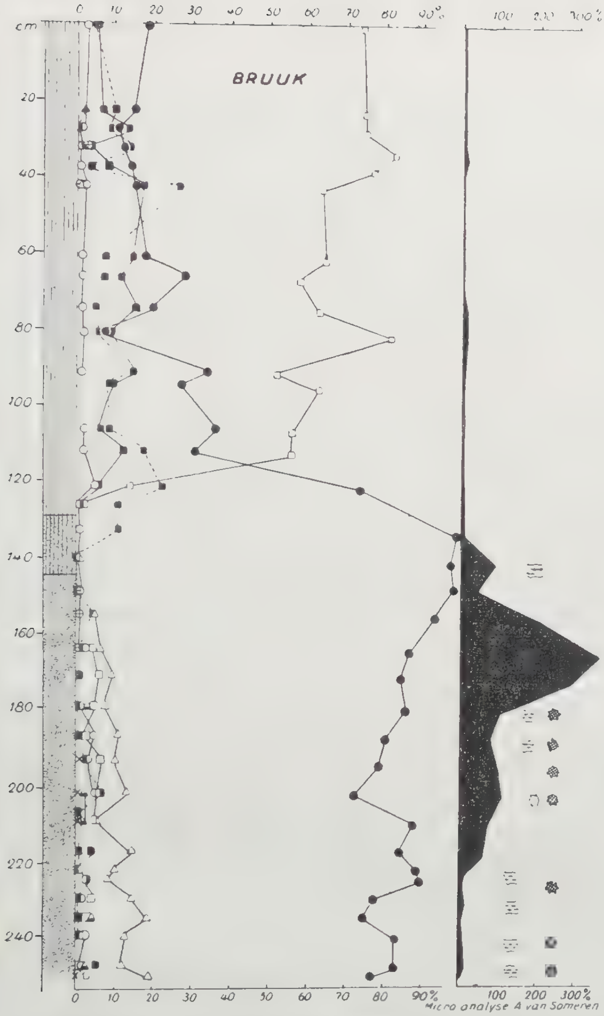
Op deze plek heeft dus eerst deflatie plaatsgehad en wel vermoedelijk in Würm I of Würm II, toen de gletschers dichter bij ons land kwamen dan in Würm III. Het zand en het stof werden naar het westen weggeblazen; het zand kwam als dekzand eerder tot rust dan de aeolische fractie, die verderop als löss neerkwam. Later, toen het deflatiegebied oostelijker lag, had hier inflatie plaats: het lössdek werd afgezet.

Het bijgevoegde pollendiagram van het Bruuk omvat löss en veen.

Het lössgedeelte vertoont, naast *Pinus*, *Picea*, *Abies*, *Carpinus*, *Betula*, *Alnus*, de componenten van het *Quercetum mixtum* en *Corylus*. Dit, gecombineerd met het ontbreken van *Fagus*, duidt op een afzetting in het laatste interglaciaal of in een interstadium van het Würmglaciaal.

Op bovengenoemde geologische gronden meen ik het Riss-Würm-interglaciaal te mogen uitsluiten. Blijven dus de twee interstadia van de Würm: I—II en II—III. Was de löss hier in het eerste interstadium afgezet, dan kan moeilijk begrepen worden, hoe ze aan de erosie in het tweede stadium weerstand heeft kunnen bieden. Meer voor de hand ligt de veronderstelling, dat de löss afkomstig is uit het laatste interstadium en wel uit het einde daarvan, toen aanvankelijk nog bossen aanwezig waren met thermophiele bomen. Geleidelijk werden de bossen lichter en het thermophiele hout werd schaarser. Een nieuwe phase van de ijstijd was aangebroken. Misschien komt in dit deel van het diagram de toendra tot uiting, maar het is ook denkbaar, dat afzettingen uit het stadiale maximum ontbreken. Zeker is dat het geval met afzettingen uit de eerste twee perioden van het Laatglaciaal. Uit de derde, het Praeboreaal in engere zin, is misschien de venige löss afkomstig. Het veen is holoceen: boreaal en jonger.

Zo maken geologische en palynologische overwegingen het waarschijnlijk, dat de Gelderse löss afkomstig is uit het laatste interstadium en misschien uit het laatste stadium van het Würmglaciaal. Dit is niet in overeenstemming met de mening van Tesch, die in



— **Diagramme pollinique du loess et de la tourbe de Bruuk.**

Explication des signes employes dans le diagramme

▥ Tourbe ▥ Tourbe argileuse ▨ Loess

—□— Alnus ‑‑■‑‑ Corylus —×— Abies

—○— Betula —●— Pinus —⊕— Salix

—△— Picea —▲— Carpinus —▲— Fagus

—■— Quercetum mixtum (Quercus Tilia et Ulmus)

▶ Gramineae, Cyperaceae, Ericaceae et varia

≋ Radicelles de Carex ◌ Myriophyllum ✺ Pediastrum boryanum

Mededeling I van de Toelichtingen bij de Geologische Kaart van Nederland (1942) zegt, dat hij de lössachtige, stoffijne afzetting, die de binnenhellingen van de stuwwal tussen Velp en Dieren en tussen Ubbergen en de Plasmolen bekleedt, beschouwt als een bezinksel van verplaatste löss in een stuwmeer tijdens de afsmelting van het landijs van het Riss-glaciaal.

Daarna behandelde Dr D. M. DE VRIES de „*Graslandtypen en hun Ecologie*", waarover hier een voorlopige mededeling volgt. Over dit onderwerp zal binnenkort een uitvoerig artikel gepubliceerd worden.

Eerst werd de methode beschreven, waarmede de typering van de Nederlandse graslanden geschiedt. Het is de plantensociologische frequentie-methode, die een behoorlijke stabiliteit der waarden waarborgt in tegenstelling tot de gewichtsanalyse en tot de methode, waarbij het aantal spruiten geteld wordt, werkwijzen, die vaak te grote verschillen geven naar de tijd, waarop men bemonstert. Om er echter voor te zorgen, dat de frequentie-methode ook van landbouwkundige betekenis is, is de vakmaat zeer klein gekozen, namelijk die van $\frac{1}{4}$dm^2. Dan is men er van verzekerd, dat de hoog frequente soorten ook in gewichtsaandeel minstens van betekenis zijn, d.w.z. dat dit laatste 5% of meer bedraagt. Deze soorten kan men dan ook potentieel gewichtig noemen. Voor de gebezigde methode zij verder verwezen naar de volgende artikelen: *Methods of determining the botanical composition of hayfields and pastures.* Rep. Fourth Intern. Grassl. Congr., p. 474—480, XII 1937, Aberystwyth; *The plant sociological combined specific frequency and order method.* Chron. Bot., 4, 2, p. 115—117, IV 1938, Leiden.; *De verenigde aanwezigheids- en rangorde-methode.* Ned. Kruidk. Arch., 48, p. 48—51, XI 1938, Amsterdam.

Van alle voor de typering in aanmerking komende soorten is nagegaan, welke frequentie-grens zij moeten bereiken om tot de potentieel gewichtige te kunnen worden gerekend. Deze grens bedraagt normaal 50%, voor grove soorten en pollenvormers echter 25% en voor de gelijkmatig verspreide, fijne ondergrassen *Poa pratensis L.* en *P. trivialis L.* 75%.

Ter typering zijn die soorten gekozen, welke in landbouwkundig opzicht veelzeggend zijn, d.w.z. een goede, slechte of matige grasmat aangeven, en (of) bruikbare indicatoren zijn in oecologisch opzicht. Er worden onderscheiden *hoofdtypen* naar 1 typerende soort, *typen* naar 2 en *ondertypen* naar 2 of meer typerende soorten. Bijgaande sleutel, opgesteld volgens een voorkeur-stelsel, geeft een overzicht der typering van de bijna 400 onderzochte, niet zilte graslanden.

Intussen zijn de twee volgende mededelingen, met overeenkomstige inhoud, over de typering verschenen: *Method and Survey of the characterization of Dutch grasslands.* Vegetatio, Acta Geobot., 1, 1, p. 51—57, VII 1948, 's-Gravenhage; *De botanische samenstelling van Nederlandse graslanden.* I. *De typering van graslanden.* Versl. van Landbouwkundige Onderz., 54, p. . . . . ., 1948, 's-Gravenhage Hierin is ook een bespreking van de landbouwkundige waardering en oecologie van de hoofdtype- en type-vormers opgenomen ter motivering van hun keuze. Karakteristiek voor deze typering is, dat hare eenheden te beschouwen zijn als combinaties van frequente indicatoren.

Aan het botanisch onderzoek van de percelen grasland van ons type-onderzoek ging gepaard grondonderzoek, verricht door het Bedrijfslaboratorium voor Grondonderzoek, van de voor oud grasland zo belangrijke bodemlaag van 0—5 cm diepte, waarin de plantenvoedende stoffen zijn opgehoopt, terwijl verder aantekeningen werden gemaakt omtrent de vochtigheidstoestand, behandeling en het gebruik van het land. De fosfaat- en kalitoestanden van de grond werden als slecht (s), onvoldoende (ov), matig (m), voldoende (v) of goed (g) beoordeeld. De pH-waarden zijn in de volgende zuurgraadsklassen ondergebracht: zeer sterk zuur (zsz, pH < — 4.0), sterk zuur (sz, 4.1—5.0), matig zuur (mz, 5.1—5.5), zwak zuur (zz, 5.6—6.0). bijna neutraal (bn, 6.1—7.0) en alkalisch (a, > 7.0). De grondsoorten zijn globaal onderscheiden in veen (v, > 30% humus), venige grond (vg, 21—30% hum.), klei (k, > 40% afslibbaar), zavel (zl, 11—40% afsl.), zand (z, < = 10% afsl.). Teneinde een indruk te hebben van het vocht- en basenbindend vermogen van de grond werden de percentages klei-humus (% humus + $\frac{1}{4}$% afslibbaar) berekend en in de volgende klassen ingedeeld: I (0—20% kh), II (21—40%), III (41—60%), IV (61—80%) en V (81—100%). Daarnaast werd ruwweg de vochtigheidsgraad van het grasland te velde aangeduid als droog (d), normaal vochthoudend (nv), vochtig (v) of nat (n). Als voornaamste gebruikswijzen werden onderscheiden: echt hooiland (eh), hooiweide (hw), wisselweide (ww) en echte weide (ew). Echt hooiland en echte weiden worden alleen maar gehooid (1, 2 of 3 sneden) resp. beweid. Hooiweiden worden jaarlijks een keer gehooid en daarna beweid, ook wel voorbeweid. Wisselweiden worden sommige jaren alleen beweid, andere jaren gehooid.

Bijgaande tabel geeft een voorlopige indruk van de voorkeur van de belangrijkste hoofdtypen betreffende bovengenoemde factoren. De afkortingen geven aan voor welke toestand, klasse enz. er van voorkeur sprake is, waarbij die voor eerstgenoemde het duidelijkst uitkomt.

Voorkeur hoofdtypen grasland betreffende milieu-factoren.

Hoofdtypen	P toe-stand	K toe-stand	pH	Grond-soort	Klei-hum. klass.	Vocht-graad	Ge-bruiks-wijze
Lolium perenne	v-g	g	bn-zz	k-zl	II-I	nv	ww-ew
Poa trivialis	g-v	m-g	bn-zz		II-I	v-nv	hw
Poa pratensis	v-g	v-g	bn-zz	z	I	nv-d	ew
Alopecurus prat.	g-ov	m	a-zz	k	II	nv-v	hw-ww
Holcus lanatus	s-ov	m	zz	z-v	I-III	v	eh-hw
Festuca rubra	ov-m	m	bn-mz	z-zl-k	I-II	nv-d	ew-eh
Agrostis s + t	s-m	m-v	mz	k-vg	II	v-nv	ew-ww
Agrostis canina	s-ov	m-s	mz	v-vg	IV	v	eh-hw
Molinia coerulea	s	s-ov	mz-sz	v	IV	v-n	eh

Sleutel der graslandtypering.

Op de horizontale rij bovenaan staan de soorten vermeld, welke bij voldoende frequentie hoofdtypen van die naam vormen. Zij zijn genummerd in de volgorde van voorrang, die bovendien door pijlen is aangegeven.

De verticale rij links geeft de soorten, welke bij de onderverdeling der hoofdtypen een rol spelen. Bij de bepaling van hun voorrang doen zich twee gevallen voor. Het ene geval, aangegeven door nummering en pijlen links, treft men aan, wanneer een der hoofdtypen 1 t/m 6 of 13 t/m 17 is gevonden; het andere geval, aangegeven door nummering en pijlen rechts, treft men aan, wanneer men met een der hoofdtypen 7 t/m 12 te maken heeft.

In het overzicht zijn de door ons gevonden typen ingevuld, benevens het aantal keren, waarin zij geconstateerd zijn.

Op de horizontale rij beneden vindt men het aantal percelen van elk hoofdtype.

Betekenis der afkortingen van de soorten, welke bij de typering een rol spelen, met hun frequentie-procent-grenzen tussen haakjes:

Lp = Lolium perenne L. (50)
Pt = Poa trivialis L. (75)
Pp = Poa pratensis L. (75)
Ap = Alopecurus pratensis L. (25)
Arr = Arrhenatherum elatius J. A. C. Presl. (25)
D = Dactylis glomerata L. (50)
Pha = Phalaris arundinacea L. (25)
Ag = Alopecurus geniculatus L. (50)
Hl = Holcus lanatus L. (50)
Fr = Festuca rubra L. (50)
A = Agrostis stolonifera L. + tenuis Sibth. (50)

			1						3				2						
				2	3	4	5	6	13	14	15	16	12	11	10	9	8	7	
			Lp	Pt	Pp	Ap	Arr	D	Ag	Hl	Fr	A	Cyp	Ao	Ac	Fo	M	N	
1	1	Lp	Lp-Lp 1																
	2	Pt	Lp-Pt 37	Pt-Pt 5															
	3	Pp	Lp-Pp 1	Pt-Pp 10	Pp-Pp														
	4	Ap	Lp-Ap 4	Pt-Ap 6															
	5	Arr			Pp-Arr 1	Ap-Arr 1	Arr-Arr 1												
	6	D	Lp-D 2				Arr-D 2												
3	7	Pha		Pt-Pha 1		Ap-Pha													3
	8	Ag	Lp-Ag	Pt-Ag 6									Cyp-Ag 1		Ac-Ag 1				
	9	Hl	Lp-Hl 2	Pt-Hl 8						Hl-Hl 1				Ao-Hl 5	Ac-Hl 1	Fo-Hl 1			
	10	Fr	Lp-Fr 4	Pt-Fr 5	Pp-Fr 8	Ap-Fr	Arr-Fr	D-Fr		Hl-Fr	Fr-Fr 8		Cyp-Fr 2		Ac-Fr 1		M-Fr 4		
4		A	Lp-A 27	Pt-A 17	Pp-A 5	Ap-A		D-A	Ag-A	Hl-A	Fr-A 19	A-A 15			Ac-A 1	Fo-A 1			
	10	Fa									Fr-Fa 1								2
	9	Gf											Cyp-Gf 1						
	8	Dc	Lp-Dc 1									A-Dc 1			Ac-Dc 1				
	7	Gm		Pt-Gm 1															
2	6	Cyp		Pt-Cyp 5									Cyp-Cyp 2	Ao-Cyp 2	Ac-Cyp 4				1
	5	Ao	Lp-Ao 6	Pt-Ao 9		Ap-Ao 1									Ac-Ao 2	Fo-Ao 1			
	4	Ac		Pt-Ac 1											Ac-Ac 2		M-Ac 9	N-Ac 1	
	3	Fo															M-Fo 4		
	2	M															M-M 5	N-M 2	
	1	N																	
			161	74	15	13	8	2	1	7	28	16	6	7	13	3	22	3	

Sleutel der graslandtypering.

Trit = Triticum repens L. (50)
Fa = Festuca arundinacea Schreb. (50)
Gf = Glyceria fluitans R.Br. (50)
Dc = Deschampsia caespitosa P.B. (25)
Gm = Glyceria maxima Holmb. (25)
Cyp = (zeer vochtminnende) Cyperaceae (50)
Ao = Anthoxanthum odoratum L. (50)
Ac = Agrostis canina L. (50)
Fo = Festuca ovina L. (50)
M = Molinia coerulea Moench. (50)
N = Nardus stricta L. (25)

De laatste spreker was Dr F. P. Jonker, die sprak over

Botanische bijdragen tot het onderzoek van holocene transgressie en regressie.

De eerste botanische aanduiding van een regressie van de zee was de grenslaag van Weber, die in onze hoogvenen het atlantische oude mosveen scheidt van het subatlantische jonge mosveen. In de tijd waarin deze grenslaag afgezet is, het subboreaal, moet de veengroei practisch stil gestaan hebben door het uitdrogen van de hoogvenen.

In de bodem van het Westen van ons land vinden we op vele plaatsen tussen de oude blauwe zeeklei en de jonge zeeklei een veenlaag, het oppervlakteveen, dat ook van subboreale ouderdom is. Zo komen we dus tot de aanname van een daling van de zeespiegel in subboreale tijd, die in het Oosten van ons land de grondwaterstand zodanig verlaagde, dat de veengroei stil stond. In het Westen trok de zee zich terug, zodat op het eerst door de zee overspoelde gebied zich een riet- en moerasvegetatie vormde, die aanleiding werd tot veenvorming.

In het daaropvolgend subatlanticum transgredeerde de zee weer. Het grondwater in het oosten steeg en de veengroei begon opnieuw. In het Westen overstroomde de zee het veenlandschap en zette de jonge zeeklei af.

Het onderzoek van de profielen uit de tunnelput bij Velzen en van enkele andere plaatsen in West Nederland gaf aan FLORSCHÜTZ en spr. het inzicht dat ook in het midden-boreaal een regressie moet plaats gehad hebben. Het grondwater was toen nl. daar ter plaatse zo hoog gestegen dat zich op het laagterras een *Alnetum* vestigde, waarvan de overblijfselen aangetroffen werden. De wortels van deze elzen zijn toen 3 m het zand ingedrongen omdat het grondwater over die afstand daalde. Op het niveau, 18 m onder NAP heeft het toen lange tijd een vaste stand gehad. Daarna steeg het grondwater weer, inundeerde de oppervlakte van het laagterras, waarna de lagunaire afzettingen ontstonden, die we nu het veen op grotere diepte noemen. Dit werd in de loop van het atlanticum, als gevolg van de steeds stijgende zeespiegel overstroomd en bedekt met mariene sedimenten (oude blauwe zeeklei en oudzeezand). Vroeger noemde men deze overstroming de oud-holocene transgressie. Het is echter geen plotselinge catastrophe maar een phase in de voortdurende stijging van de zeespiegel en het vond niet plaats in het oud-holoceen maar in het atlanticum.

Tussen 1905 en 1939 werd in N.W. Duitsland eenzelfde onderzoek verricht door de kwartair-geoloog SCHÜTTE, die daar eveneens een midden-boreale en een subboreale regressie vond en bovendien nog een midden-atlantische. In Engeland bestudeerde de palaeobotanicus GODWIN deze verschijnselen tussen 1938 en 1945. Hij vond een regressie (althans een stagnatie in de transgressie) in het midden-atlanticum, de subboreale regressie en bovendien nog aanwijzingen voor een regressie in historische tijd.

In het laat-glaciaal en in de eerste helft van het boreaal steeg dus bij Velzen de zeespiegel tot het laagterras voltooid was en het oppervlak daarvan moerassig werd. Deze laat-pleistocene en vroeg-boreale transgressie is te vergelijken met transgressie I van SCHÜTTE en het zoute *Yoldia*-stadium van de Oostzee.

Omstreeks het midden-boreaal trad een regressie op toen de *Alnus* bij Velzen de lange wortels vormde. Dit is regressie I van SCHÜTTE, het zoete *Ancylus*-stadium van de Oostzee. GODWIN vond deze regressie niet.

In de tweede helft van het boreaal trad opnieuw een transgressie op, voortdurend in het Atlanticum, waarin het veen op grotere diepte, de wadafzettingen en de oude zeeklei gevormd werden. Dit is transgressie II en III van SCHÜTTE, het zoute *Littorina*-stadium van de Oostzee. Een regressie tijdens deze periode, regressie III van SCHÜTTE, kon niet aangetoond worden.

In het subboreaal treedt een regressie in, regressie III van SCHÜTTE, de eerste duidelijke regressie van GODWIN, het zoete *Limnaea*-stadium van de Oostzee. Dan volgt in het subatlanticum weer een transgressie, transgressie IV van SCHÜTTE, het zoute *Mya*-stadium van de Oostzee. De mogelijkheden en bezwaren van parallelisatie van de resultaten in Nederland en die van GODWIN werden besproken en de uitkomsten van het Nederlandse onderzoek aan de hand van graphische voorstellingen vergeleken met die uit N.W. Duitsland en Engeland. Tenslotte werden enkele berekeningen gegeven over de gemiddelde stijging van de zeespiegel per eeuw.

VERSLAG van de Achttiende Nederlandse Dag voor Biosociologie en Palaeobotanie, gehouden op 15 December 1946 in de Collegezaal van het Botanisch Laboratorium te Utrecht.

Nadat de voorzitter, Dr A. SCHEYGROND, de achttiende „sociologendag" met een kort woord geopend had, gaf hij het woord aan de eerste spreker, Dr M. F. MÖRZER BRUYNS, die sprak over

De Molluskenfauna van het Naardermeer.

De Molluskenfauna van het Naardermeer wordt in het onderhavige onderzoek van biosociologisch standpunt bekeken. Er is nagegaan „hoe" deze dieren in het meer voorkomen, welke soorten en hoe talrijk zij in de belangrijkste plantengezelschappen leven. botanisch onderzoek van VAN ZINDEREN BAKKER heeft daarbij tot leiddraad gediend. Aangezien de waarnemingen hebben plaats gehad van 1941—1944, zijn de veranderingen, die de landslakkenfauna na de inundatie van 1945 heeft ondergaan, niet in het onderzoek betrokken.

In een tiental plantengezelschappen werden een aantal opnamen gemaakt; de quantitatief faunistische inventarisatie volgde op de plantensociologische beschrijving. Het uitzeven en tellen van de mollusken was een zeer tijdrovende bezigheid. Enkele plantengezelschappen, b.v. het *Scirpeto-Phragmitetum* zijn niet onderzocht, aangezien dat zonder bijzondere hulpmiddelen niet mogelijk was. Hieraan moet worden toegeschreven dat een aantal soorten, die reeds van vorige onderzoekingen (VAN DER SLEEN, VAN REGTEREN ALTENA, VAN BENTHEM JUTTING en KUIPER) bekend waren niet zijn aangetroffen. Aan de andere kant leverde het onderzoek de vondst op van *Planorbis leucostoma* en *Punctum pygmaeum*, beide „nieuw" voor het Naardermeer. De volgende levensgemeenschappen werden onderzocht. 1. Het „gezelschap van *Naias marina* en *Nitellopsis obtusa*" in de Bovenste Blik. Hierin leefden talloze *Valvata piscinalis* en *Pisidium spec.*, veel *Planorbis albus*, *Physa fontinalis* en *Lymnaea ovata* en enige *Bithynia tentaculata*. In een „open" vorm van het *Myriophylletum-Nupharetum* werden de volgende soorten aangetroffen: *Valvata piscinalis*, *Bithynia leachi* en *tentaculata*, *Planorbis planorbis*, *P. carinatus*. *P. vortex* en *vorticulus*, *P. contortus*, *P. albus*, *P. crista* en *P. complanatus* en tenslotte *Lymnaea stagnalis* en *L. ovata*. In het typische waterlelie-plompgezelschap kwamen behalve deze soorten eveneens *Valvata cristata*. *Acroloxus lacustris*, *Planorbis corneus* en *Segmentina nitida* voor. Aangezien het aantal waarnemingen gering is, mag men nog geen conclusies trekken over eventuele voorkeur voor bepaalde begroeiingen.

In het *Hydrochareto-Stratiotetum* ontbrak *Valvata piscinalis*, waren de andere soorten goed vertegenwoordigd en traden *Lymnaea palustris* en *Myxas glutinosa* als nieuwe slakken op.

In de oevergezelschappen van het *Cicuteto-Caricetum pseudocyperus* nemen de waterslakken in aantal sterk af, alleen *Planorbis planorbis* en *P. contortus*, *Segmentina nitida* en *Lymnaea palustris* zijn nog talrijk. De landslakken doen hun intrede met 7 soorten. *Succinea pfeifferi* alleen is in de drogere biotopen niet meer aangetroffen, *Carychium minimum*, *Vertigo antivertigo*, *Succinea putris*, *Acroceras laeva*, *Retinella lammonis*, *Zonitoides nitidum*, *Euconulus trochiformis* en *Arianta arbustorum* wel, al is er nog duidelijk onderscheid tussen de mollusken-populaties van het *Magnocaricion*, het *Molinion* en het *Alnion*. *Cochlicopa lubrica*, *Arion ater*, *Arion circumscriptus* en *Vitrea crystallina* zijn b.v. tot beide laatste gezelschappen beperkt. *Goniodiscus rotundatus* kwam slechts voor op één plaats in een Moliniongezelschap. Opvallend slakkenarm zijn het voedselarme *Caricetum inflato-vesicariae* en het mesotrophe *Betuleto-Salicetum*. *Arion intermedius* geeft duidelijk aan het laatstgenoemde bostype de voorkeur. Voor de tweekleppigen moge worden verwezen naar de desbetreffende publicaties van VAN BENTHEM JUTTING en KUIPER.

De volgende spreker was Dr L. TINBERGEN, die sprak over *Vegetatie en Vogelbevolking.*

De verspreiding over verschillende landschapsvormen gaat bij vogels, evenals bij andere bewegelijke dieren, principieel anders in zijn werk dan bij vele planten. Bij de laatste worden de diasporen in kwistige hoeveelheid over een groot gebied verspreid; of een bepaald individu tot ontwikkeling komt hangt af van de levenskansen, die het milieu biedt. Vogels daarentegen selecteren actief hun milieu; zij oefenen met hun zintuigen en zenuwstelsel een voortdurende contrôle uit op de terreinvormen, waarin zij zich begeven en verlaten deze, zodra ze hun niet meer aanstaan. Het vraagstuk van de veroorzaking van de verspreiding heeft dus een psychologisch aspect; men kan zich afvragen, aan welke kenmerken een vogelsoort zijn geliefde milieu onderscheidt. Een definitief antwoord op deze vraag kan slechts het experiment geven. Dit vond nog weinig toepassing. Een mooi voorbeeld levert het werk van PALMGREN op. Een grauwe vliegenvanger (vogel van de peripherie der boomkruinen en der open ruimten in het bos) meed in een proefkooi een model van „struweel", dat bestond uit een groot aantal parallel aangebrachte zitstokjes met geringe onderlinge horizontale en verticale afstand. Eerst wanneer deze afstand sterk vergroot werd, kwam de vogel in het „kunstmatig struweel". Een spotvogel (bewoner van dichte struikachtige begroeiingen en van het inwendige der boomkronen) bewoog zich daarentegen ook bij geringe onderlinge afstand der stokjes tussen deze. De fijnheid der vertakking is dus voor deze twee vogelsoorten essentieel bij de keuze van hun plaats van oponthoud.

Een dergelijk experiment zet de kroon op het verspreidingsonderzoek, dat begint met het opzoeken van correlaties tussen het voorkomen van een vogelsoort en de eigenschappen van de vegetatie.

Men kan deze correlatie trachten te leggen met „synthetische" kenmerken van de begroeiing, dus met de naam van de plantenassociatie. Voor een bepaalde vogelsoort zou men een spectrum van associaties kunnen opstellen, waarin zij voorkomt. Voor descriptieve doeleinden is dit aardig, omdat de naam van de associatie ons een korte code geeft voor vele eigenschappen van het biotoop.

Stellen wij ons niet tevreden met een descriptieve doelstelling, maar willen wij de veroorzaking van de verspreiding uitwerken en dus de mogelijke kenmerken nagaan, waaraan de vogel zijn soort-eigen milieu onderscheidt, dan leidt de vaststelling van de naam van de plantenassociatie ons op een dood spoor. Wij moeten dan de vegetatie, waarin de vogelsoort leeft, naar verschillende gezichtspunten gaan analyseren. Ten dele kan hierbij de sociologische opname van nut zijn, ten dele moeten andere eigenschappen van de begroeiing in het geding gebracht worden. Uit de plantensociologische opnamen kan blijken, of er correlatie met het voorkomen van bepaalde plantensoorten of -combinaties is. Zulke bindingen zijn zeldzaam.

Met welke andere eigenschappen van de vegetatie correlaties gezocht moeten worden, kan het beste na bestudering van de levenswijze van de vogelsoort in kwestie vastgesteld worden. Men gaat dus alle levensfuncties bekijken met de vraagstelling: welke eigenschappen van het terrein maken het de vogel mogelijk om deze functies uit te voeren en welke verhinderen dit? In de regel blijken de volgende eigenschappen van belang te zijn: voedselrijkdom, nestelgelegenheid, gelegenheid voor slapen en dekking vinden tegen roofvijanden en de mogelijkheid voor de voortbeweging. De laatste vier bijzonderheden hangen vooral af van de structuur van de begroeiing.

Ofschoon onderzoek volgens deze principes zelden ver doorgevoerd is en een synthese dus prematuur lijkt, kunnen we toch nagaan of het mogelijk is groepen van vogels met ongeveer gelijke terreineisen op te stellen, die men als „vogelassociaties” kan beschouwen. Het meest rationele standpunt lijkt mij slechts een klein aantal grotere groeperingen op te stellen. Beperkt men zich bijv. tot de broedvogelfauna der struik- en boomrijke landschappen, dan blijkt de soortensamenstelling van de vegetatie vrij weinig invloed op de aard van het aanwezige vogelgezelschap uit te oefenen; haar ontwikkelingsvorm en ruimtelijke structuur des te meer. Zo vindt men in struikvormige begroeiingen, onverschillig of deze uit hakhout, uit jonge aanplanten van naald- en loofhout of uit de struikétage van een rijk bos bestaan, een vogelgezelschap, waarvoor fitis, tuinfluiter, roodborst, merel en zanglijster karakteristiek zijn. Voor volgroeide bomen, onverschillig hun soort, zou men de vink, de tjiftjaf en de koolmees karaktersoorten kunnen noemen. Desnoods zou men de hier genoemde vogelassociaties nog iets verder kunnen indelen. De struikgroep zou men in een natte variant (met rietzangers) en een droge variant (zonder deze soorten), in een lage (met grasmus) en een hoge (met tuinfluiter) kunnen indelen; de boomgroep in één van open bos (met boompieper) en één van gesloten bos (zonder deze soort) kunnen splitsen, maar in feite daalt men dan weer af tot de verspreiding van afzonderlijke soorten. Heel onwaarschijnlijk lijkt het mij ten slotte, dat men de indeling zo kan inrichten, dat men een samenvallen van bepaalde vogelgroeperingen met bepaalde plantenassociaties kan verkrijgen.

Dit alles gold alleen de soortensamenstelling van de vogelbevolking. De soorten van één „vogelassociatie” komen bovendien in verschillende biotopen in verschillende dichtheid voor. De dichtheid van de soorten van de boomgroep stijgt bijv. met toenemende mengingsgraad en met toenemende hoogte der bomen. Deze dichtheidsverschillen zijn in de eerste plaats terug te brengen op sterkere en zwakkere voorkeur voor bepaalde biotopen. De vraag, waardoor het algemene niveau van de bevolkingsgrootte bepaald wordt, ligt ten slotte op een heel ander plan: dat der evenwichten tussen voortplanting en sterfte. Hier spelen de levenskansen een directe rol.

Als derde spreker kreeg hierna het woord Dr E. M. VAN ZINDEREN BAKKER, die een mededeling deed over *Pollenanalyse van Veluwse Venen.* Hiervan werd geen resumé ontvangen. De vierde spreker was Ir G. SISSINGH over *De levensvormen van onze akkeronkruiden en de levensvormenspectra der akkeronkruiden.* Ook van deze voordracht werd geen verslag ontvangen; verwezen kan worden naar de binnenkort verschijnende dissertatie van spr. De vijfde en laatste spreker was de heer J. VAN DER DRIFT, die sprak over

De bodemfauna in bossen.

De bodem van onze bossen, waartoe, behalve het minerale substraat, hier ook de oppervlakkige strooisellaag wordt gerekend, wordt bewoond door een dierenwereld, die zeer veelzijdig van samenstelling is. Alle aan het terrestrische leven aangepaste stammen van het dierenrijk zijn in de bodemfauna vertegenwoordigd. Dit houdt in dat de afmetingen van de dieren uiteenlopen van enkele honderdste millimeters tot meer dan een decimeter. Ook de levenswijzen van de dieren variëren sterk. Naast dieren die hun hele levenscyclus in de bodem doorbrengen (*geobionten*) zijn er soorten die dit slechts gedurende een of enkele stadia doen (*geophielen*).

Wat is de betekenis van deze bodemfauna in de samenleving van het bos?

Ter beantwoording van deze vraag moeten we eerst de samenstelling van de dierlijke levensgemeenschap in de bodem in quantitatief opzicht leren kennen.

Voor een onderzoek hiernaar moeten zeer verschillende methoden worden toegepast.

Voor zover de fauna in voldoende dichtheid voorkomt kan ze onderzocht worden in monsters. De *microfauna* (kleiner dan 0,2 mm, *rhizopoden*) moet onderzocht worden in opgeslibde monsters van enkele mm^3. De *mesofauna* (0,2—2 mm) wordt onderzocht in monsters van 40 cm^3. De voornaamste vertegenwoordigers van deze groep zijn mijten en springstaarten. Door een geleidelijke uitdroging van de monsters worden deze dieren voor een zeer groot percentage gevangen. *Nematoden, tardigraden* en *rotatoriën*, die ook tot de *mesofauna* behoren, worden gevangen met behulp van een uitspoeltechniek. Voor het grootste deel van de *macrofauna* (2—20 mm, wormen, *myriapoden*, vliegenlarven, kevers, spinnen enz.) wordt ook een uitdrogingstechniek toegepast. De grootte van deze monsters bedraagt 4 dm^3. Voor soorten die in te geringe dichtheid voorkomen om in deze monsters in voldoende aantallen gevangen te worden wordt een andere techniek gebruikt: in het terrein van onderzoek worden op een oppervlak van b.v. 50 × 50 m, van de betrokken soorten gemerkte exemplaren vrijgelaten en deze tegelijk met de autochthone dieren in ingegraven bussen gedeeltelijk teruggevangen. Uit de verhouding van gemerkte en niet gemerkte dieren en het aantal vrijgelaten gemerkte dieren is hun dichtheid bij benadering vast te stellen. Van de *megafauna* (groter dan 20 mm, muizen, *insectivoren*) kan ook met behulp van de terugvangsttechniek de dichtheid van voorkomen worden bepaald.

Op deze wijze kunnen we ons een beeld vormen van de quantitatieve samenstelling van de dierlijke levensgemeenschap in de bodem op een bepaald ogenblik. Natuurlijk is het hierbij noodzakelijk, voor zover het onderzoek betrekking heeft op monsters, deze monsters uit de verschillende onderscheidbare lagen (strooisel-, humus- en zandlaag) afzonderlijk te nemen. Hierbij blijkt dat de meeste soorten een specifieke verticale verspreiding hebben, die door klimaatsfactoren (droogte, vorst) echter sterk beïnvloed kan worden.

Hoewel de frequentiepercentages van de soorten met de grootste dichtheid meestal zeer hoog zijn, kunnen de aantallen in verschillende parallelmonsters vaak zeer sterk uiteenlopen. Voor het vaststellen van seizoensfluctuaties is dan ook steeds een groot aantal parallellen noodzakelijk.

Voor verschillende microarthropoden konden duidelijke fluctuaties worden vastgesteld. Van de geophiele macrofauna komt de phaenologie van de soorten uit de vangstresultaten duidelijk naar voren. Ook de vangkuilmethode geeft een goed inzicht in de phaenologie van bodemkevers en -spinnen.

Is de samenstelling van de fauna en haar fluctuaties gedurende het jaar bekend, dan is het mogelijk van de belangrijkste soorten de levenswijze door kweken na te gaan. Van de saprophage soorten kunnen zo quantitatieve gegevens betreffende de strooiselomzetting verkregen worden. Uit deze gegevens, de dichtheid van voorkomen en de jaarlijks vallende hoeveelheid strooisel is het mogelijk de betekenis van deze soorten bij de strooiselomzetting in getallen weer te geven. Het blijkt dat een aanzienlijk deel van het jaarlijks vallend strooisel door deze soorten wordt opgevreten.

Bij van roof levende dieren moeten we ons voorlopig beperken tot qualitatieve waarnemingen. Dat de talrijke loopkevers op de zich in de bodem verpoppende schadelijke insecten een belangrijke invloed uitoefenen is echter zeer waarschijnlijk.

VERSLAG van de Commissie voor de Bescherming van de Wilde Flora over 1946.

Het jaarverslag over 1946 van de Commissie voor de Bescherming van de wilde flora heeft weinig van betekenis te melden.

De activiteit ten bate van het behoud van het Nederlandse natuurschoon, die wij in het verleden ontwikkelden, wordt gaandeweg meer en meer overgenomen door speciale organisaties. Dat was destijds al de op onze instigatie tot stand gekomen „Contactcommissie inzake natuurbehoud”.

Thans kan gememoreerd worden het tot stand komen van de „Natuurbeschermingsraad”, een belangrijke stap vooruit bij vroeger, toen wij door tussenkomst van de Adviescommissie van het Staatsbosbeheer reeds menigmaal een botanisch interessant terrein konden bewaard zien.

Via Contactcommissie en Natuurbeschermingsraad kunnen wij thans opkomen voor die terreinen, wier behoud niet alleen botanisch, maar ook zoölogisch, geologisch of recreatief van betekenis is. Wij zelf kunnen ons dan beperken tot de alleen botanisch belangrijke plekken.

Zo hadden wij dit jaar attentie voor de *Parietaria*-vegetatie op oude muren te Amersfoort, die bij een beraamde schoonmaak gevaar loopt te verdwijnen.

Dan heeft onze commissie gemeend in te moeten gaan op een artikel in „Natura”, waarin de schrijver zich voorstander betoonde van het uitzaaien en uitplanten van wilde gewassen op terreinen, waar deze niet van nature voorkomen. Ook al wordt aan ons of aan het I.V.O.N. opgave verstrekt van de uitgezette planten, dan moeten wij ons daartegen verklaren. Dit kan slechts leiden tot vervalsing van het natuurlijke vegetatie-beeld.

TH. WEEVERS, Voorzitter.
JAN G. SLOFF, Secretaris.

VERSLAG van de Commissie voor de Phytopathologie over 1946.

In Januari 1946 werd in de vacature, ontstaan door het periodiek aftreden van Mej. Dr J. C. WENT voorzien door de verkiezing van ondergetekende, die het secretariaat overnam. Tevens trad Mej. Dr L. C. DOYER af als lid van de Commissie en werd vervangen door Dr J. W. M. ROODENBURG.

2 November 1946 werd op het Laboratorium „W. Commelin Scholten" te Baarn een druk bezochte vergadering gehouden, waar gesproken werd door de heren:

Dr H. G. VAN DER WEIJ over Phytopathologische aspecten der Delische tabakscultuur;

Dr P. A. VAN DER LAAN: Motschildluis en Eupatorium als oorzaken van pseudo-mozaiek in Deli-tabak;

Dr W. F. VAN HELL. Mouldy Rot, een schimmelziekte van het tapolak;

Dr A. PFÄLTZER: Moeilijkheden door het niet-slagen van kunstmatige infectie met sporen.

Wageningen, 13 Januari 1947.

De Secretaresse,
CAROLINE H. KLINKENBERG.

VERSLAG van de Commissie voor de Physiologie over 1946.

De Commissie, in September '46 opgericht, hield zijn eerste bijeenkomst op Zaterdag 9 November in het Botanisch Laboratorium te Utrecht. Aanwezig waren 18 leden. Dr L. W. KUILMAN sprak over Physiologische onderzoekingen over rijst.

Amsterdam, 31 Dec. 1946.

De Secretaris,
A. W. H. VAN HERK.

VERSLAG van de Vergadering der Commissie voor Plantensystematiek en -geografie op Zaterdag 16 November 1946.

Alle Commissieleden zijn aanwezig, te weten: Dr CH. H. ANDREAS, Dr J. TH. HENRARD, Dr H. J. LAM, Dr J. LANJOUW, Dr S. J. VAN OOSTSTROOM en Dr A. A. PULLE.

Laatstgenoemde wordt tot voorzitter, Dr ANDREAS tot secretaresse benoemd. Volgorde en jaartallen van aftreden worden bij loting als volgt bepaald: Dr PULLE 1948, Dr ANDREAS 1949, Dr HENRARD 1950, Dr LAM 1951, Dr LANJOUW 1952, Dr v. OOSTSTROOM 1953.

Er zal eenmaal per jaar, in Maart, een bijeenkomst worden gehouden.

Plannen worden besproken voor een in Nederland te houden voor-congres van systematici, vermoedelijk in 1948, voorafgaande aan het Botanisch Congres te Stockholm in 1950.

De Secretaresse,
CH. H. ANDREAS.

VERSLAG van de Commissie van Redactie voor de Flora Neerlandica over 1946.

Een ernstig verlies leed de Commissie van Redactie door het plotseling overlijden van haar secretaris Dr W. H. WACHTER, die als zodanig in de bezettingstijd Dr J. HEIMANS was opgevolgd. Dr WACHTER heeft zijn beste krachten aan de Flora gegeven door niet alleen een aantal families zelf te bewerken, doch ook door een groot deel van de manuscripten van andere medewerkers op zijn accurate wijze persklaar te maken. Zijn plaats in de Commissie zal wederom door Dr HEIMANS worden ingenomen. De Commissie werd aangevuld met één lid, Dr Ir A. W. KLOOS Jr.

Op een subsidieaanvrage aan het Ministerie van Onderwijs, Kunsten en Wetenschappen werd een hoopvol antwoord ontvangen; in principe bleek men bereid te zijn de gevraagde subsidie te verlenen; over de wijze waarop dit geschieden zal wordt nog gecorrespondeerd.

De manuscripten van alle families voor het eerste deel der Flora, dat de Pteridophyten, de Gymnospermen en de Monocotylen zal bevatten, zijn thans in handen der redactie. Voor het grootste deel zijn zij reeds persklaar gemaakt. Moeilijkheden in de personeelsbezetting bij de drukker en gebrek aan voldoende materiaal waren tot nu toe de oorzaak, dat niet met het zetten begonnen kon worden. Zeer onlangs werd echter van de drukker de toezegging verkregen, dat nu regelmatig aan het zetten zal kunnen worden gewerkt, zodat de hoop bestaat, dat aan het eind van 1947 het 1e deel het licht zal kunnen zien.

Oegstgeest, Februari 1947. De waarnemend-secretaris,
S. J. VAN OOSTSTROOM.

NOTULEN over 1946.

JAARVERGADERING op Zondag 27 Januari 1946, in het Botanisch Laboratorium te Utrecht.

Op de huishoudelijke vergadering zijn aanwezig: 2 introducé's, de heren A. H. G. G. RIJVEN en P. TIDEMAN; en 54 leden, nl. de dames en heren: ARISZ, VAN ASPEREN DE BOER, P. J. BELS, BELS-KONING, BOK, BOTTELIER, BREMER, FLORSCHÜTZ, GODDIJN, C. GORTER, A. GORTER, HEIMANS, VAN HERK, HOF, HOMBURG, HUECK, P. JANSEN, JASPERS, JONKER, KARSTENS, KLINKENBERG, KLOOS, KONINGSBERGER, KRUYT, G. KRUSEMAN, LANJOUW, DE LEEUW, J. C. LINDEMAN, MARGADANT, MELTZER, NIEUWENHUYZEN, VAN OOSTSTROOM, PIET, QUISPEL, TER PELKWIJK, ROMBOUTS, ROODENBURG, SIRKS, J. C. SOBELS, SPIERENBURG, STAFLEU, VAN DER STEEN, SWART, THIERENS, TJALLINGII, VAROSSIEAU, VERHOEF, WACHTER, WEEVERS, WESTHOFF, WESTERDIJK, DE ZEEUW, VAN ZINDEREN BAKKER.

Dr KONINGSBERGER opent om 11 uur de vergadering. Hierbij herdenkt hij de leden, die in de afgelopen maanden overleden zijn: Professor Dr L. H. SIERTSEMA en Mevrouw Dr C. H. VAN HARREVELD-LAKO. In Januari heeft te Leiden de erepromotie plaats gehad van de ereleden der Vereniging JANSEN, KLOOS en WACHTER. De voorzitter memoreert dit heuglijke feit en feliciteert de heren namens de Vereniging met hartelijke en zeer waarderende woorden.

De notulen van de vorige vergadering worden na voorlezing goedgekeurd.

De eerste Secretaris bracht op de vorige vergadering, welke de eerste was na de bevrijding, een kort verslag uit over de lotgevallen van de vereniging in de periode van Februari 1944 tot October 1945. Thans geeft hij hierop een aanvulling; samen vormen deze verslagen het concept-jaarverslag voor 1944 en '45, hetwelk wordt goedgekeurd.

De ontwerp-jaarverslagen van de permanente Commissies worden voorgelezen en goedgekeurd.

De rekening en verantwoording van de Penningmeester over 1944 en '45 worden goedgekeurd. Naar aanleiding van de begroting voor 1946 merkt Dr VAN DER STEEN op, dat het Zoölogisch Station te Den Helder de laatste 2 jaren geen subsidie heeft gehad. Daar men a.s. zomer weer een cursus wil houden is er veel geld nodig voor de wederopbouw. Dr v. D. STEEN stelt voor de pro-memoriepost op de begroting te veranderen in een werkelijke post en deze bovendien te verhogen. Dr JANSEN plaatst *f* 200.— op de begroting. Dr WEEVERS brengt de Contactcommissie nog eens onder de aandacht: zij heeft reeds gezorgd voor het behoud van floristisch belangrijke terreinen. In de toekomst zal de activiteit van de Commissie duidelijker naar buiten blijken, daar men een tijdschrift wil gaan uitgeven; ook heeft de Commissie een veldbiologisch archief gesticht. *f* 50.— wordt op de begroting geplaatst.

De voorzitter dankt de Penningmeester en ook zijn voorganger, die de Vereniging met haar belangrijk kapitaal zo meesterlijk door de moeilijke jaren heen geloodst hebben.

De Heer WESTHOFF vraagt om continuering van de contributie voor de Commissie voor internationale Natuurbescherming, welke ook pro-memorie op de begroting voorkomt; de Commissie heeft het plan een bioloog aan te stellen. Er komt *f* 50.— op de begroting.

In de Commissie tot nazien van de rekening en verantwoording en de bescheiden van de Penningmeester worden benoemd de heren CROOCKEWIT en HEIMANS.

Thans gaat men over tot de benoeming van nieuwe leden. Het voorstel tot benoeming van Ir J. W. VAN DIJK, hetwelk voorkomt op de convocatie, wordt ingetrokken; alle overigen worden benoemd. Op de vergadering zelve worden nog voorgesteld Dr W. M. KRUSEMAN en J. RIETSEMA; beiden worden benoemd.

De voorgestelde leden van de permanente Commissies worden allen benoemd. Op de convocatie komen enkele voordrachten niet voor; deze worden op de vergadering bekend gemaakt, zodat nog de volgende benoemingen of herkiezingen plaats hebben:

In de Commissie van Redactie van het Recueil des Travaux botaniques, vacature Dr K. ZIJLSTRA: herkozen.

In de Commissie voor Floristiek, vacature Ir J. L. VAN SOEST: herkozen. In de Sub-Commissie voor Zuiderzeeonderzoek, vacature Dr G. KRUSEMAN: herkozen. De Sub-Commissie wordt aangevuld met H. W. E. CROOCKEWIT en J. MELTZER.

In de Commissie voor de Bescherming van de Wilde Flora wordt benoemd in de vacature G. A. BROUWER (niet herkiesbaar): V. WESTHOFF; in de vacature Dr J. P. THIJSSE: Dr J. HEIMANS.

In de Commissie van de Biosociologie, vacature van de Voorzitter, Dr A. A. PULLE, wordt benoemd: Dr A. SCHEYGROND.

Thans wordt over de benoeming van de voorzitter der Vereniging gestemd, nl. in de vacature Dr V. J. KONINGSBERGER. Twee en vijftig stemmen worden uitgebracht, waarvan zes en dertig op Dr ARISZ, vijftien op Dr LAM en 1 blanco, zodat Dr W. H. ARISZ benoemd is tot voorzitter. Dr ARISZ neemt de benoeming aan.

De Commissie voor de Plantenphysiologie komt ter sprake. De Voorzitter licht het Bestuursvoorstel toe. De steeds grotere specialisatie van de verschillende takken der botanische wetenschap maakt het wenselijk, deze takken in afzonderlijke Commissies bijeen te roepen, waar detailproblemen behandeld kunnen worden, die voor de beoefenaars der andere takken van minder direct belang zijn. Het is de bedoeling naast de Commissie-vergaderingen een of twee maal per jaar algemene wetenschappelijke vergaderingen te houden, welke voor alle leden interessant zijn. Hier moeten dan sprekers optreden, die een groter gebied overzien. Enkele leden, waaronder Dr WEEVERS en Dr SWART, betreuren de steeds grotere splitsing, waardoor het onderling contact tussen de leden zoveel geringer wordt. Verschillende leden brengen hiertegen in, dat men juist zo een bizonder sterk onderling contact aantreft in de reeds bestaande Commissies.

Professor WESTERDIJK en de heer A. GORTER vinden, dat de Plantenphysiologen dezelfde rechten hebben als de Sociologen, Phytopathologen e.a. De Vereniging moet hun het recht gunnen een eigen Commissie te stichten. Daar de grote meerderheid der vergadering het voorstel toejuicht, wordt dit aangenomen.

Er zal nu ook een Commissie voor de Plantensystematiek moeten komen.

Dr KONINGSBERGER neemt nu afscheid als voorzitter, terwijl Dr ARISZ met enkele inleidende woorden zijn taak overneemt.

Om 12.30 uur wordt de Vergadering geschorst voor het gebruiken van de lunch, waarna om 2 uur de wetenschappelijke Vergadering aanvangt. Thans zijn aanwezig 5 introducé's, nl. de dames en heren: A. G. BRUNNER, E. BRUNNER-DE VRIES, GOBEE, J. TH. SOBELS-BIERMANS, J. DE TEMPE en 86 leden. Sedert de ochtendvergadering zijn hierbij gekomen de dames en heren: L. BELS, VAN BEVERWIJK, BOEKE, S. DE BOER, G. BRINK, LE COSQUINO DE BUSSY, VAN EYNDHOVEN, W. VAN ITERSON, G. JANSEN, A. M. DE JONG, KREGER, W. KRUSEMAN, LENS, LÖHNIS, LODDER, MILTENBURG, NICOLAI, OFFERIJNS, OOMEN, OPPENOORTH, VAN DER PLAATS NITERINK, D. E. RIJNDERS, RIJVEN, STAKMAN, TIDEMAN, UYLDERT, P. VERMEULEN, V. DE. VRIES, WASSINK, WENT, DE WILDE, WYBRANS.

Dr KONINGSBERGER houdt een voordracht over „Zeventig jaren antibiose; Penicilline”.

LEDENVERGADERING op Zondag 1 September 1946 in het Botanisch Laboratorium te Amsterdam, Plantage Middenlaan (Indische Dag).

Op de ochtend-vergadering zijn aanwezig 12 introducé's, nl. de dames en heren: G. E. BADENHUIZEN-BENJAMIN, J. VAN BORSSUM WAALKES, R. BRINK, G. BUWALDA, E. E. HARMSEN, F. W. OSTENDORF, C. M. OSTENDORF-DOYER, M. J. VAN STEENIS-KRUSEMAN,

G. VERRIEST? (uit Gent; naam niet duidelijk leesbaar), W. A. DE VOOGD, H. F. DE VRIES en een onleesbaar. Voorts 83 leden: de dames en heren: ALBERDA, ANDREAS, ARISZ, VAN ASPEREN DE BOER, C. A. BACKER, D. BAKKER, BELS-KONING, L. BELS, BEUMEE, BEIJER, BOK, BOSHUIZEN, BOTTELIER, BREMER, G. BRINK, BROUWER, BUNSCHOTEN, DRION, VAN EYNDHOVEN, GIESBERGER, GROENHIJUZEN, I. DE HAAN, HEIMANS, VAN HELL, VAN HERK, HOF, VAN DEN HONERT, HONING, HOUWINK, IDENBURG, G. VAN ITERSON, P. JANSEN, JASPERS, A. M. JONG, PH. DE JONG, KARSTENS, KLEINHOONTE, KLEIJN, KLOOS, G. KRUSEMAN, W. M. KRUSEMAN, KRUYT, VAN DER LAAN, LAM, LANJOUW, A. D. J. MEEUSE, MOOI, MULDER, F. M. MULLER, OFFERIJNS, VAN OLDEN, VAN OOSTSTROOM, PIET, VAN DER PLAATS-NITERINK, POLAK, PRAKKEN, PULLE, QUISPEL, VAN RAALTE, E. REINDERS, REINDERS-GOUWENTAK, ROELOFSEN, ROODENBURG, SALVERDA, SCHURE, VAN SLOGTEREN, VAN STEENIS, SWART, TOXOPEUS, TIDEMAN, TAMMES, VAN DER VAART, VAROSSIEAU, WASSCHER, WASSINK, WEEVERS, WENT, VAN DER WERFF, WESTERDIJK, VAN DER WEIJ, DE WILDE, F. WIT, DE ZEEUW, ZEIJLEMAKER, VAN ZINDEREN BAKKER; en 2 onleesbaar.

Om half elf opent de Voorzitter, Dr ARISZ, de vergadering, die een bizonder karakter draagt, daar zij geheel aan Indië gewijd is. Dr ARISZ spreekt over de activiteit van de groep leden in Indië, gedurende de jaren '40 tot '42, toen zij van het moederland afgesloten waren. Hij toont het eerste nummer van de Mededelingen van de Nederlandsche Botanische Vereeniging van Maart 1941, dat dank zij het initiatief van verschillende leden in Indië, waaronder vooral Dr POSTHUMUS, Dr V. D. HONERT en Dr VAN STEENIS, tot stand is gekomen en het onderling contact bewaard heeft. Ter gedeeltelijke vervanging van het Recueil en het Ned. Kruidkundig Archief ontvingen de leden overdrukken als bijlage bij deze „Mededeelingen". Helaas hebben de meeste medewerkers, vroeger of later na de Japanse overval, het werk moeten neerleggen. Dr O. POSTHUMUS is na de capitulatie van Japan door extremisten gevangen genomen en hoogstwaarschijnlijk gedood. Hetzelfde lot trof Mevrouw Dr C. H. VAN HARREVELD-LAKO; van Dr A. RANT kwam eveneens het overlijdensbericht binnen. Tijdens zijn leven bestudeerde hij het Indische plantenleven en publiceerde veel in de „Tropische Natuur".

Ook in Nederland zelve heeft de Vereniging, sedert de laatste vergadering doden te betreuren: Mejuffrouw Dr E. G. C. TALMA en de Heer M. C. E. STAKMAN, beiden werkzaam bij het middelbaar onderwijs; Ir N. VAN POETEREN, Directeur van de Plantenziektenkundige Dienst, die één jaar vóór de pensioengerechtigde leeftijd overleed. Hij was een bekende figuur, ook in het buitenland, waar hij Nederland vertegenwoordigde in vele Commissies en op conferenties op phytopathologisch gebied.

De notulen van de vorige vergadering worden gelezen en goedgekeurd.

Het schriftelijk verslag van de Kascommissie vermeldt, dat alle bescheiden van de Penningmeester in goede orde bevonden zijn.

De op de convocatie voorkomende aspirant-leden worden allen benoemd. Bovendien worden nog benoemd de dames en heren: Dr R. BRINK, Mejuffrouw B. BUILLAB, T. BURGER, E. S. C. VAN DAM, H. REEDIJK, D. VREUGDENHIL, D. NOORDAM, allen tijdens de vergadering voorgesteld door het Bestuur. Verder C. DOETS, voorgesteld door G. KRUSEMAN, S. J. VAN OOSTSTROOM, D. PIET.

Naar aanleiding van het voorstel tot instelling van een Commissie voor de plantensystematiek en -geographie wijst de Voorzitter op het gevaar, dat in het algemeen aan het vormen van secties verbonden is, nl. dat hierbij de mening zou kunnen post vatten, dat de problemen van een sectie niet thuis horen op een algemene vergadering. Dit is geenszins het geval: alle problemen van de botanie zijn belangrijk voor de gehele vereniging. Op een Commissie-vergadering kunnen zij echter een meer uitgebreide en meer gedetailleerde behandeling vinden dan op een algemene vergadering mogelijk is. Indien men dit goed voor ogen houdt, is er geen bezwaar tegen het instellen van commissies. Ir KLOOS waarschuwt voor de kans, die bestaat, dat verschillende Commissies op hetzelfde tijdstip een vergadering zouden uitschrijven, waardoor de vereniging als het ware uit elkaar zou worden getrokken. Het Bestuur zal hieromtrent een voorziening treffen, zodat de voorzitters der Commissies steeds contact houden met de algemene Voorzitter.

Het voorstel tot instelling van de Commissie voor de Plantensystematiek en -geographie wordt dan zonder verdere discussie aangenomen.

Het Bestuur neemt het voorstel tot wijziging van artikel 54 der statuten, betreffende het bewaren van bibliotheek en Herbarium, voorlopig terug. Ten aanzien hiervan behoeven nog andere artikelen, o.a. 28, wijziging; dit alles zal op de jaarvergadering behandeld worden. De overige wijzigingen worden aangenomen.

De reglementen van de Commissies worden vastgesteld, zoals zij op het convocatie-biljet voorkomen.

De voorgestelde leden der nieuwe Commissies worden allen benoemd.

Na afhandeling van bovengenoemde kwesties gaat men over tot de wetenschappelijke vergadering. Als eerste spreker treedt op: Dr H. J. TOXOPEUS met een voordracht over:

Botanisch onderzoek aan het Plantkundig Instituut van het Algemeen Proefstation voor de Landbouw te Buitenzorg.

Spreker geeft eerst een kort overzicht van de gang van zaken gedurende de Japanse bezetting in het Buitenzorgse wetenschappelijke milieu. Hiervoor kan worden verwezen naar de betreffende mededelingen in het Natuurwetenschappelijk Tijdschrift, waarvan op 1 Juni 1946 het eerste nummer na de bevrijding: Dl. 102, Afl. 3, weer is verschenen.

Daarna volgt een overzicht van de wording van het Algemeen Proefstation voor de Landbouw, waarvan het Plantkundig Instituut één der vier delen is. Onderstaand schema geeft aan, hoe deze organisatie voor de Japanse bezetting en sedert 1928 werkte.

Organisatie en bezetting met academisch gevormd personeel van het Algemeen Proefstation voor den Landbouw te Buitenzorg.

Directoraat	1
Instituut v. Plantenziekten, leiding	1
Mycologische afdeling	4
Dierkundige afdeling	4
Cultuur-technisch Instituut, leiding	1
Afdeling overjarige gewassen	3
Afdeling eenjarige gewassen	5
Landbouwkundige afdeling	5
Proeftuinen v. d. Tuinbouw	2
Bodemkundig Instituut, leiding	1
Bodemkundig laboratorium	6
Bodemkartering	10
Plantkundig Instituut, leiding	1
Genetisch laboratorium	2
Physiologisch laboratorium	1
Microbiologisch laboratorium	1
Totaal Academici	48

Het Algemeen Proefstation voor de Landbouw is een gouvernementsinstelling en houdt zich bezig met het onderzoek van problemen van de inlandse landbouw en van die cultures, welke door de Europese landbouw worden gedreven en die zelf niet over een proefstation beschikken. Voorts is een belangrijke taak het onderzoek van de mogelijkheden voor nieuwe handelsgewassen.

Het plantkundig instituut heeft officieel tot taak:

1. Het uitvoeren van plantkundige onderzoekingen ten behoeve van de werkzaamheden van verschillende onderdelen van het Departement van Economische zaken.

2. Zich op de hoogte houden van de vorderingen van de botanische wetenschap, met het oog op de mogelijkheden van toepassing daarvan in eigen werk of in het werk van andere instellingen.

Daar het aantal belangrijke gewassen van de inlandse land- en tuinbouw groot en de botanische kennis daarvan over het algemeen gering is, is het werkprogram overvoerd. Er kan met de relatief zwakke bezetting van 5 academici en 3 middelbare krachten slechts oriënterend onderzoek worden verricht.

Het onderzoek is in 3 richtingen gedifferentiëerd:

a. in genetische richting, ten behoeve van de veredeling (Dr H. J. Toxopeus, Dr F. Wit, Dr A. G. van der Meulen).
b. in physiologische richting, ten behoeve van de rijstcultuur, en veredeling (Dr L. W. Kuilman).
c. in bacteriologische richting, ten behoeve van het onderzoek naar de betekenis der leguminosen en — onder drang der omstandigheden — ten behoeve van de industrie (Dr Ph. de Jong).

Kort werkprogram van de genetische afdeling in de laatste jaren.

Citrus:	Polyembryonie en vegetatieve vermeerdering, zelf- en kruisingssteriliteit.
Kapok:	Bloembiologie, ecologie van de vruchtzetting, geographische verspreiding.
Derris:	Hybridisatie, variabiliteit van de wilde populatie, cytologie.
Aleurites:	Biologie van de bloei en de vruchtzetting, soortskruising, variabiliteit.
Amorphophallus:	Mangaangehalte van de wilde soorten, ecologie, zaadzetting van A. oncophyllus.
Kruidnagel:	Variabiliteit van de wilde en de gekweekte vorm, periodiciteit, bladval, beurtdracht.
Sereh:	Systematiek, embryologie, hybridisatie-mogelijkheden.
Peper:	Systematiek, variabiliteit, biologie van de vruchtzetting, hybridisatie-mogelijkheden.
Strophantus:	Oorzaken van het uitblijven der vruchtzetting, zelf- en kruisings-steriliteit.
Aardappelen:	Hybridisatie-mogelijkheden van Solanum tuberosum met verwante soorten.
Mangga:	Polyembryonie en vegetatieve vermeerdering, techniek van de hybridisatie, minimumfactoren voor de vruchtzetting.
Bataten:	Zelf- en kruisings-steriliteit, mogelijkheden voor de veredeling.

Hibiscus:	Mogelijkheden van soortkruisingen voor de veredeling van de vezelsoorten.
Katoen:	Hybridisatie van soorten van de oude- en van de nieuwe wereld.
Boehmeria:	Biologie van de zaadvorming, techniek van de hybridisatie.
Broussonetia:	Biologie van de zaadvorming.

De genetische afdeling heeft grote behoefte aan een ervaren cytoloog. Bij practisch elk gewas is nl. het onderzoek naar de vorming van de gameten en de zygoten van overwegend belang.

Speciaal de physiologische afdeling heeft behoefte aan verdere uitbouw. Een begin is door Dr KUILMAN gemaakt met een onderzoek naar de transpiratie van de rijst in verband met irrigatie-problemen. Dit is een zeer omvangrijk werk, daar men met allerlei rijstvariëteiten onder verschillende omstandigheden van bodem en klimaat moet werken. Iets dergelijks zal ook gedaan moeten worden voor de verdamping van de zeer belangrijke tweede gewassen, als mais, soja, aardnoten en cassave, die in de droge tijd dikwijls bevloeiing nodig hebben. Dit voert tot een uitgebreid onderzoek naar de ontwikkeling van het wortelstelsel van deze gewassen. Hiermede werd eveneens een begin gemaakt. Voorts heeft een nader onderzoek van de uitloging van het blad van gecultiveerde planten en vooral ook van de wilde vegetatie grote betekenis voor een goed begrip van de balans van de vruchtbaarheid van de bodem.

Vervolgens spreekt Dr B. POLAK over:

Veen en Veenonderzoek in de Indische Archipel.

Tot het begin van de twintigste eeuw werd veenvorming in een tropisch klimaat voor onmogelijk gehouden, omdat men meende, dat tengevolge van de hoge temperaturen, afgestorven plantendelen snel en volledig zouden worden afgebroken.

Deze opvatting werd herzien, toen in 1895 het verslag van de IJZERMAN-expeditie, „Dwars door Sumatra", verscheen, waarin KOORDERS beschrijft, hoe deze expeditie te kampen had met het doortrekken van uitgestrekte woudvenen, begroeid met dicht bos op dikke veenlagen. Naar aanleiding hiervan publiceerde POTONIÉ in 1905 een studie: „Die Sumpfflachmoornatur des produktiven Karbons". Hierin wordt de mening verkondigd, dat in de tropen alleen onder water afgezet veen kan voorkomen, laagveen dus; en dat hoogveenvorming is uitgesloten, omdat hiervoor de verdamping te groot is.

Recente onderzoekingen hebben echter aangetoond, dat in Indië althans, zowel ombrogene, oligotrophe hoogvenen voorkomen als laagveen: topogeen veen.

De ombrogene venen worden regionaal aangetroffen langs de Oostkust van Sumatra, langs de kusten van Malakka en langs de Westkust van Borneo. Plaatselijk ook aan de Westkust van Sumatra en de Oostkust van Borneo, terwijl ook aan de Zuidkust van Nieuw-Guinea uitgestrekte hoogvenen voorkomen. Deze gebieden, nl. Sumatra, Malakka en Borneo, waren eens door het Soenda-plat verbonden; Zuid Nieuw Guinea bezat in het pleistoceen een grote uitbreiding in het Sahoelplat.

Aangenomen kan worden, dat het onderlopen dezer platten in het holoceen het ontstaan der regionale moerassen heeft veroorzaakt.

De regionale woudvenen zijn zeer zuur, nl. pH = 3; bruin gekleurd water stroomt er aan alle zijden af. Het centrum ligt hoger dan de randen, zoals waterpas-metingen hebben aangetoond en waarnemingen ter plaatse doen zien. Het gehalte aan kalk en N, P, K komt overeen met dat van bekende Europese oligotrophe venen. Dit doet tot het ombrogene karakter besluiten.

Topogene venen worden plaatselijk in de gehele archipel aangetroffen. Op Java vindt men geen andere. In het gebergte is wel is waar *Sphagnum* algemeen, doch het is geen veenvormer. De topogene venen zijn hoofdzakelijk door kruiden opgebouwd: grassen, *Cyperaceae* en varens, *Susum malayanum* enz. Plaatselijk komen ook hout-overblijfselen voor.

Tijdens de Japanse bezetting is van spreekster een studie over een topogeen veen op Java, de Rawah Labok in Zuid Priangan, verschenen. Het onderzoek wees uit, dat de waterstand gedurende de vorming van het veen is gestegen. Merkwaardig is een laag zuivere vulkanische as, van circa 40 cm dikte, die op een diepte van ongeveer 50-80 cm onder het maaiveld voorkomt. Tijd noch herkomst van deze eruptie kon worden vastgesteld. Ware dit het geval geweest, dan hadden wij de snelheid van de veengroei kunnen bepalen.

Daar het thans over enen is, wordt de voordracht van Dr VAN DER WEIJ uitgesteld tot na de lunch.

Na de koffiemaaltijd heropent de Voorzitter circa half drie de vergadering. Thans zijn aanwezig 5 introducé's (behalve de dames en heren van hedenmorgen nog één onleesbaar) en 78 leden. Nog gearriveerd zijn: de dames en heren BADENHUIZEN, BOEDIJN, S. DE BOER, HOMBURG, B. DE JONG, KOSTER en VAN DER PIJL.

De Voorzitter doet eerst de ontstellende mededeling, dat Dr W. H. WACHTER, op weg naar de vergadering, plotseling overleden is. Dr Wachter was pas benoemd tot erelid der vereniging en had te Leiden het doctoraat honoris causa in Januari van dit jaar ontvangen. Deze gebeurtenis zal zeker zijn stempel drukken op deze reeds bizondere bijeenkomst. Dr Weevers schetst het leven van Dr Wachter en spreekt over de buitengewoon grote betekenis, die deze voor de vereniging gehad heeft. In de eerste plaats is dit de verzorging van het Kruidkundig Archief gedurende meer dan 25 jaren. Het gedenkboek bij het 100-jarig bestaan van de Vereniging, dat binnenkort verschijnen zal, is bijna geheel van zijn hand.

Het overlijden van Dr Wachter maakt een diepe indruk op de vergadering.

Dr H. G. van der Weij houdt een voordracht over:

Autonome parthenogenese bij Deli-tabak.

Gevonden werd, dat Deli-tabak autonoom parthenogenetisch zaad kan voortbrengen. De beste methode bleek te zijn: het doorknippen van de bloembuis, zodra deze uitgegroeid is. Uit het parthenogenetische zaad ontwikkelden zich fertiele — en voor zover dit is nagegaan — diploide planten, die onderling en ten opzichte van de moederplant soms duidelijke verschillen vertoonden. Apogamie is dus niet aannemelijk. In aansluiting op hetgeen elders bij geinduceerde parthenogenese is gevonden lijkt het waarschijnlijk, dat het diploide zaad zich heeft ontwikkeld uit echte, dus haploide eicellen na chromosomenverdubbeling in het jonge embryo. Indien dit vermoeden juist is, zullen er zo uit een bastaard-moeder uitsluitend homozygote kinderen ontstaan, waarbij het aantal genotypen gelijk is aan dat der haploide genencombinaties. Door het winnen van parthenogenetisch zaad wordt getracht om de eigenschap „verhoogde resistentie tegen slijmziekte", die tot nu toe volkomen niet-zaadvast was, in homozygote vorm te verkrijgen. Of dit mogelijk is, kon evenwel nog niet worden vastgesteld.

Hierna volgt de voordracht van Dr P. A. Roelofsen, getiteld:

Overzicht van recent onderzoek aan het Deli proefstation voor tabak.

In verband met noodzakelijke beperking wordt alleen besproken het werk der laatste jaren, voor zover het op botanisch gebied lag en tot de hoofdonderwerpen van het werkprogramma behoorde. Aan de hand van verschillende voorbeelden wordt toegelicht hoe men in de tabakscultuur bij bestrijding van ziekten en plagen steeds weer rekening moet houden met beïnvloeding van de kwaliteit van de tabak, die buitengewoon gevoelig is. Van het werk der plantkundige afdeling wordt besproken: onderzoek van gebrekverschijnselen in watercultures met een zodanig verbeterde methodiek, dat normale planten van 2 m hoogte in 2 maanden werden verkregen. Aangetoond is, dat wanneer ter bestrijding van boriumgebrek in de praktijk meer dan 6 mg boorzuur per plant gegeven wordt, de kwaliteit benadeeld kan worden.

Vroeger deed gewoon mozaïek veel schade, nu niet meer dan 1%, dank zij door het proefstation gepropageerde maatregelen. Belangrijker wordt pseudomozaïek, dat door *Bemisia* overgebracht wordt van onkruiden, die rondom de tabaksaanplant staan en waarvan *Eupatorium odoratum* de voornaamste is. Van de plantaardige ziekten is de belangrijkste: slijmziekte door *Bacterium solanacearum* veroorzaakt en waartegen op resistentie wordt geselecteerd. Belangrijk is ook spikkel, een bladvlek-ziekte door *Cercospora*, die door Cu-fungiciden bestreden kan worden, ware het niet, dat de tabak het koper in sporen opneemt en een slechte kleur en smaak ervan krijgt.

De landbouwkundige afdeling heeft als hoofdpunt: onderzoek naar de meest gewenste bemesting op de verschillende grondsoorten, hetgeen gedaan wordt met behulp van veldproeven, bodemanalyse en gewas-analyse. Er openen zich hier nieuwe terreinen van onderzoek door het op de markt komen van nieuwe meststoffen en de door de plantkundige afdeling verkregen aanwijzing, dat met neutrale meststoffen inplaats van zure, de slijmziekte beter bestreden zal kunnen worden. Het gaat veeleer om de verbetering van de kwaliteit dan om verhoging der opbrengst. Daarom zijn veldproeven volgens de gebruikelijke methoden niet mogelijk, want de beoordeling der kwaliteit gaat volgens subjectieve methoden: op het oog, het gevoel en de smaak.

Van groot belang zijn ook de onderzoekingen ter verhoging van de bodemvruchtbaarheid en andere landbouwkundige maatregelen ter bestrijding der slijmziekte. Het is nodig na tabak de grond 7 jaar braak te laten liggen onder bos, daar men anders slechte tabak en veel ziekte krijgt. Eenzijdige begroeiing, b.v. met *Mimosa invisa* kan minder slijmziekte geven, maar geeft ook slechter kwaliteit. Daarom wordt gestreefd naar gemengd kunstmatig bos, dat bestaat uit elementen, die geen slijmziekte kunnen herbergen en zo mogelijk ook nog wat opbrengen. Bos maakt de grond het vruchtbaarst in de tropen.

Tenslotte spreekt Dr F. WIT over:

Bloei en vruchtdracht bij Aleurites montana Wils.

Aleurites montana Wils. en *A. fordii Hemsl.* zijn 2 boomsoorten, die in China sinds eeuwen worden gekweekt ten behoeve van de uit de zaden geperste olie, de Chinese hout-olie of tung-olie. Deze verscheen aan het eind van de vorige eeuw als concurrent van de lijnolie op de wereldmarkt. De productie in China nam daarna enorm toe. Sedert 1930 tracht men de *Aleurites*-cultuur in Indië te vestigen. Daarbij bleek *A. fordii* al spoedig voor deze streken ongeschikt; *A. montana* bood iets gunstiger perspectieven. In 1937 werd aan het Plantkundig Instituut van het Algemeen Proefstation voor de Landbouw een algemeen botanisch onderzoek van *Aleurites* opgedragen, als grondslag voor selectie- en cultuuronderzoek. Het zwaartepunt viel daarbij op de processen, die de vruchtdracht bepalen: bloei, bestuiving, bevruchting en vruchtzetting.

A. montana is éénslachtig en éénhuizig, met een neiging tot tweehuizigheid. Naast import-aanplantingen van gemengde bloeiers met een varierend % vrouwelijke bloemen, komen nl. aanplantingen voor van zeer overwegend manlijke en vrouwelijke bloeiers. De bloeigewoonte bleek in de opvolgende jaren vrij constant, en voornamelijk bepaald door de erfelijke aanleg van de boom. Inverschillende aanplantingen werd een nauwe correlatie gevonden tussen wijze van bloei en productie. De opbrengst was bij de overwegend manlijke bomen gemiddeld slechts $^{1}/_{9}$ van die der overwegend vrouwelijke. Omstreeks 70% der import-bomen behoort tot de eerste groep en is daardoor voor de cultuur al waardeloos. In goede aanplantingen moeten dergelijke bomen dus worden geweerd.

Uit de bloei-waarnemingen volgt, dat *A. montana* overwegend kruis-bestoven wordt en in het algemeen niet zaadvast zal zijn. Vegetatieve voortplanting van de moederbomen biedt dus voorlopig betere perspectieven dan generatieve. Bepaalde zaaisels kunnen echter zoveel productieve bomen bevatten, dat ze voor de praktijk te gebruiken zijn. Wegens het overheersen van kruisbestuiving bij de meeste moederbomen zijn spontane zaaisels daarvoor ongeschikt; in enkele daarvan werd reeds een hoog percentage manlijke bomen aangetroffen. Men dient uit te gaan van legitiem zaad van goede moederbomen, ontstaan na zelfbestuiving, of na kruising met een goede vader.

De bestuiving geschiedt door insecten. In clonen-aanplantingen, (en misschien ook in sommige legitieme zaaisels) kan de manlijke bloei zó gering zijn, dat niet voldoende vrouwelijke bloemen kunnen worden bestoven. In één clonen-aanplant werd reeds de bestuiving als beperkende factor voor de dracht onderkend. In dergelijke aanplantingen dient men dus voor pollenproducenten te zorgen.

Zelfbestuiving gaf steeds dezelfde slaging als kruisbestuiving; zelfincompatibiliteit werd dus niet waargenomen. Evenmin werd bij de vele kruisbestuivingen kruisings-incompatibiliteit geconstateerd.

Men behoeft derhalve in clonen-aanplantingen niet bang te zijn voor verminderde vruchtzetting als gevolg van bestuiving met eigen of niet passend pollen.

Vruchtzetting wordt in hoge mate bepaald door de omstandigheden gedurende de eerste 6 weken na de bestuiving. In dit stadium is het zaadgewicht slechts enkele % van het vruchtgewicht, zodat de zetting bij grootzadige bomen wellicht weinig minder zal zijn dan bij kleinzadige.

Daar het zaadgewicht boomsgewijs sterk variëert, zullen dan grootzadige bomen meer produceren en zal selectie op zaadgrootte van belang zijn. Het rijpe zaad is vrijwel geheel opgevuld met endosperm en omgeven door een harde zaadwand. Vorm en grootte van het zaad zijn reeds vastgelegd voor het endosperm zijn eigenlijke groei begint. Het zijn dus kenmerken van de moederplant. Een invloed van de vader op het zaadgewicht kon dan ook niet worden geconstateerd. In hoeverre olie-gehalte en -kwaliteit van het endosperm hierdoor worden beïnvloed, kon nog niet met zekerheid worden uitgemaakt. Het tot dusver geïmporteerde materiaal is zeer variabel en omvat waarschijnlijk een groot deel van de in het land van herkomst bestaande vormenrijkdom. Als uitgangspunt voor verdere selectie biedt het veel mogelijkheden. Deze zijn nog vergroot door hybridisatie van moederbomen onderling, van cultuurvormen met wilde typen en van *A. montana* met *A. fordii.* Door kunstmatige verlenging van de dag kan nl. bij de laatstgenoemde soort bloei verkregen worden.

Ruim vier uur sluit de Voorzitter de vergadering.

LEDENVERGADERING op Zaterdag 16 November 1946 in het Botanisch Laboratorium, Lange Nieuwstraat 106, Utrecht.

Aanwezig zijn 54 leden, nl. de dames en heren:

Andreas, Arisz, Badenhuizen, van Zinderen Bakker, Bels-Koning, Boedijn, S. de Boer, van Asperen de Boer, Bok, Bottelier, Bremer, Drion, Giesberger, I. de Haan, van Hell, Honing, 's Jacob, P. Jansen, Karstens, Kleinhoonte, Kloos, Koningsberger, Kruyt, van der Laan, Hille Ris Lambers, Lanjouw, Lens, J. C. Lindeman, Löhnis, Mennega, Mooi, J. R. Müller, Nicolai, Niekerk-Blom, van Ooststroom, Oppenoorth, ter Pelkwijk, Postma, Pulle, Roelofsen, Roodenburg, Salverda, Schotsman, van Soest, van der Steen, D. M. de Vries, Waes-

BERGHE, WASSINK, WEEVERS, VAN DER WEIJ, WESTENBERG, WILBRINK, DE WILDE, DE ZEEUW.

De Voorzitter Dr ARISZ opent om 14.10 de vergadering.

Na voorlezing en goedkeuring der notulen volgt de benoeming van nieuwe leden. Behalve degenen, die op het convocatiebiljet voorkomen worden nog benoemd de dames: A. VAN SCHREVEN, R. VAN NIE en O. M. VAN ANDEL, voorgesteld door het Bestuur.

Eveneens bij acclamatie worden de nieuwe commissieleden aangewezen in de vacatures, ontstaan door het overlijden van Dr WACHTER.

Thans volgt de wetenschappelijke vergadering. Dr N. P. BADENHUIZEN spreekt over:

Haploide en polyploide tabak.

Spr. behandelt de verwachtingen, die men van de productie van haploiden en tetraploiden in de praktijk mag koesteren, speciaal met betrekking tot tabak. Haploiden werden in Klaten (Proefstation voor Vorstenlandse tabak) gemaakt met het doel, een belangrijke arbeidsbesparing te verkrijgen m.b.t. het ingewikkelde selectie-schema, nodig, om kwaliteit naast resistentie tegen ziekten (lanas, mozaïek) te handhaven. Om ervaring te krijgen voor het „verdubbelen" der haploiden, werden ook diploiden aan de inwerking van colchicine en acenaphtheen onderworpen. De resultaten, welke werden gepubliceerd in Landbouw 1941, Nature **147** (1941) 577, en Natuurwetensch. Tijdschr. Ned. Indië **101** (1941) 240, klopten met de voorspellingen. „Verdubbelde" haploiden zijn theoretisch te beschouwen als ideale homozygoten. Hun waarde is echter afhankelijk van de mutabiliteit en eventuele autosyndese. In de tabak-haploiden zijn bivalenten regel. Het gevolg is reorganisatie der chromosomen door crossing-over van homologen uit het sylvestris- en tomentosiformis-complex, en dus variabiliteit in de diploide nakomelingschap, die hierin overeenkomt met een diploide F_2, op de gewone wijze ontstaan door uitwisseling in de F_1. Het wordt in gevallen, als boven voor tabak beschreven, zeer de vraag, of een „verdubbelde" haploid wel zoveel beter is dan de gewone F_2, en of men in dit geval werkelijk te doen heeft met een tijdsbesparing.

Tetraploiden leveren veel nieuw selectiemateriaal. De kwaliteit is bedorven voor sigarentabak, maar de dikke en koolhydraatrijke bladeren openen perspectieven voor de sigarettentabak. Overigens komt men na enige generaties volgens KOSTOFF reeds over het ongunstige primaire colchicine-effect heen, de fertiliteit neemt toe, de bladstructuur gaat vooruit. Van belang was het optreden van gen-mutaties na colchicine-behandeling, waarvan sommige voor de praktijk veelbelovend waren. Tabak is dus als kwaliteitsgewas en al allotetraploid met vrij veel lange chromosomen een ongunstig object voor polyploidisatie. Het tegengestelde bleek voor Java-jute als kwantiteitsgewas met betrekkelijk weinig korte chromosomen, waar de kans op chiasmata minder is, en dus bivalenten prevaleren, met als gevolg hogere fertiliteit.

Vervolgens spreekt Dr Iz. DE HAAN over:

Bijdrage tot de kennis der rubbervorming in Hevea brasiliensis.

In zijn inleiding herdacht spreker het overlijden van Mevr. Dr G. M. VAN AGGELEN BOT met wie hij tezamen op het Proefstation West-Java te Buitenzorg het onderzoek over de physiologie der rubbervorming uitvoerde.

De rubber, die bij de aanleg van de weefsels in de melksapvaten wordt afgezet, heet primair gevormde rubber in tegenstelling tot de secundair gevormde, die na voorafgaande tap in de bast optreedt. De secundaire rubbervorming maakt regelmatige tap mogelijk.

In jonge Hevea-kiemplanten blijkt de hoeveelheid rubber, die daarin gevormd wordt, evenredig te zijn met de groei, die uitgedrukt wordt in de gevormde droge stof.

Rubber moet beschouwd worden als een afvalproduct van de bij de groei verlopende processen. De plant kan rubber niet als voedingsstof benutten.

Dit blijkt uit de volgende proef: Kiemplanten werden ontdaan van de zaadlobben, ten koste waarvan ze gedurende de eerste maand van hun ontwikkeling leven, en tegelijkertijd in het donker geplaatst. Ten gevolge hiervan kan 20% minder droge stof gevormd worden, terwijl de hoeveelheid rubber gelijk aan die van normale planten is. Ook vóór het afvallen van het oude volgroeide blad wordt de rubber niet weer in de boom opgenomen, maar blijft in het blad en wordt dus daarmede afgestoten.

Bij het Hevea-blad zijn 3 perioden in de rubbervorming te onderscheiden. Gedurende de tijd, dat de bladweefsels zich ontwikkelen wordt hierin rubber afgezet; de rubbervorming komt tot stilstand wanneer het blad volgroeid is. Vanaf dit moment heeft geen rubbervorming meer plaats tot aan het ogenblik, dat de nieuwe knop gaat uitlopen. Tegelijkertijd met het uitlopen van deze knop, wanneer er dus in de bladeren reservevoedsel voor de groei gemobiliseerd wordt, heeft ook weer rubbervorming plaats.

Dit wijst er op, dat rubbervorming in verband staat met de omzettingen van de reservevoedingsstoffen die voor de groei nodig zijn. De periodieke schommelingen in de rubberproductie van een boom laten zich hierdoor verklaren.

Bij clonen met een hoge rubberproductie was het gehalte in het blad over het algemeen groter dan bij clonen met een lage productie. Het is mogelijk, dat bij jonge bomen analyses van het blad aanwijzingen zullen kunnen geven over de te verwachten rubberproductie; hiervoor zal echter een uitgebreider onderzoek aan meer materiaal nodig zijn. Mocht dit inderdaad het geval blijken te zijn, dan betekent dit een zeer belangrijke vooruitgang voor de Hevea-selectie.

Na de voordracht van Dr DE HAAN wordt een korte pauze gehouden waarin Mevr. Dr H. C. BELS KONING mededeling doet van een merkwaardige vondst van *Tuber rufum* in het winterslaapnest van een eikelmuis in een Limburgse mergelgroeve. Deze truffelsoort is nieuw voor Nederland.

Na de pauze spreekt de heer W. KRUYT over:

De invloed van groeistoffen, vitaminen, traumatinezuur, aethyleenchloorhydrine en warm-water op het enten van sierteeltgewassen.

Aangemoedigd door de successen, verkregen na toepassing van groeistoffen bij de beworteling van stekken, heeft men getracht ook bij het enten de vergroeiing tussen ent en onderstam te verbeteren door gebruik te maken van het synthetische indolylazijnzuur en dergelijke stoffen.

De eerste publicaties dateren van 1937. Als voorbeeld wordt een en ander medegedeeld van het onderzoek van MÜLLER-STOLL en KORDES bij de druif.

Eigen onderzoek werd gedurende een drietal jaren te Boskoop verricht met Dwergsparren, Juniperus en Rhododendron. Alleen het onderzoek met Rhododendron wordt besproken.

Doel van het onderzoek: 1e. Het vergroeien van de lastige vormen (de z.g. „droge” vormen) te verbeteren en 2e. het gehele proces, dat gemiddeld zeven à acht weken in beslag neemt, te verkorten, waardoor vooral in de wintermaanden een belangrijke besparing van brandstoffen het gevolg kan zijn.

Methode. Deze moet zoveel mogelijk aangepast zijn aan de praktijk. Meestal werd daarom met de groeistoffen, vitaminen en traumatinezuur de wondvlakken van onderstam, van griffel of van beide, gepenseeld. Ook lanoline-pasta's werden toegepast.

Driejarige Rhododendron ponticum-zaailingen dienden als onderstam. Na 3, 5 en 8 weken werd gecontroleerd. Anatomisch onderzoek vond voorlopig nog niet plaats.

Resultaat. Het α-naphtylazijnzuur oefent een remmende werking uit op het uitlopen van de slapende knoppen aan de onderstam, en van de knoppen aan de griffel. De callusvorming wordt maar in geringe mate verbeterd. Het indolylazijnzuur heeft een veel zwakkere uitwerking.

Penselen van de wondvlakken met traumatinezuur en de combinatie van deze stof met glutaminezuur O. 25% als co-factor gaf maar in enkele gevallen een verbetering. Penselen met vitamine B_1, C, cumarine en glucose had geen bijzondere invloed.

Een behandeling van de griffels, vóór het zetten, met aethyleenchloorhydrine-damp gedurende 2 uur had geen verbetering tengevolge. Meer succes had een proef waarbij de griffels 1 uur ondergedompeld werden in een verdunde oplossing van deze stof in water.

Het percentage goede t/m zeer sterke callusvorming neemt dan toe van 40% (onbehandeld) tot 83%, terwijl het aantal planten waarbij de knop van de griffel „schuift” van 14 stijgt tot 24 (per groep van 30 exemplaren).

Warm-water-behandeling.

Zeer goede resultaten leverde uiteindelijk een warm-waterbehandeling van de griffels op, vlak voor het copuleren. Het blijkt, dat een kort verblijf bij hoge temperatuur (2 minuten bij 53 gr. C) hetzelfde effect heeft als een langere behandeling bij lagere temperatuur (30 minuten bij 40 gr. C).

Tenslotte is nog de werking onderzocht van een gecombineerde behandeling van warm water en groeistof. De toevoeging van idolylazijnzuur gaf verbetering.

VERSLAG van de Commissie tot het nazien van Rekening en verantwoording en de bescheiden van de Penningmeester over 1946.

Ondergetekenden hebben heden ten huize van de Penningmeester rekening en verantwoording en de bescheiden van de Penningmeester gecontroleerd en in orde bevonden.

Zij stellen daarom de Ledenvergadering voor rekening en verantwoording goed te keuren en de Penningmeester te déchargeren onder dankbetuiging voor het nauwkeurige en goede beheer der financiën.

Amsterdam, 26 Februari 1947.

D. PIET.
H. H. PRELL.

VERLIES EN WINST OVER 1946.

Kok-Ankersmit-Fonds.							
Uitgaven	f	981	35	Ontvangsten	f	1242	61
Nad. Koersverschil	„	1102	28	Saldo verlies	„	841	02
	f	2083	63		f	2083	63
Brumund-fonds							
Uitgaven	f	662	66	Ontvangsten	f	986	20
Nad. Koersverschil	„	1057	—	Saldo verlies	„	733	46
	f	1719	66		f	1719	66
Vrije fondsen.							
Onkosten	f	725	—	Interest.	f	366	02
Vergaderingen	„	111	65	Contributies.	„	4810	25
Lidmaatschappen	„	523	—	Recueil	„	43	20
Crediteuren	„	2000	—	Archief	„	347	15
Comm. v. phytopath.	„	19	10	Saldo verlies	„	372	42
Comm. v. floristiek	„	31	16				
Herb. en bibl.	„	2033	78				
Nad. Koersverschil	„	495	—				
	f	5939	04		f	5939	04

BALANS 1 JANUARI 1947.

Kok-Ankersmit-Fonds.						
Effecten en Hyp.	f 32971	69	Fonds op 1 Jan. ’46		f 36504	60
Kassaldo	„ 2691	89	Saldo verlies		„ 841	02
	f 35663	58			f 35663	58
Brumund-fonds.						
Effecten	f 24458	90	Fonds op 1 Jan. ’46		f 29990	01
Kassaldo	„ 4797	65	Saldo verlies		„ 733	46
	f 29256	55			f 29256	55
Vrije fondsen.						
Interest	f 264	—	Fonds 100-jarig bestaan		f 2000	—
Contributie	„ 1206	—	Fonds Flora Neerlandica		„ 467	55
Debiteuren	„ 29	80	Vrije fonds 1-1-’46	f 8970,49		
Effecten	„ 4331	83	Saldo verlies	„ 372,42		
Kassaldo	„ 11054	22	Vrije fonds op 1-1-’47		„ 8598	07
	f 16885	85				
Crediteuren	„ 5820	23				
	f 11065	62			f 11065	62

BEGROTING 1947.

Kok-Ankersmit-Fonds.			
Opbrengst	*f* 1000,—	Onkosten	*f* 25,—
		Biolog. Station	„ 250,—
		Wahlenbergiaterrein	„ 55,—
		Sigma	„ 100,—
		Friske Gea	„ 25,—
		Nat. monumenten	„ 100,—
		Herb. & bibl.	„ 300,—
		Bijschrijven	„ 145,—
			f 1000,—
Brumund-Fonds.			
Opbrengst	*f* 800,—	Onkosten	*f* 25,—
		Comm. v. floristiek	„ 100,—
		Z.Z.-Commissie	„ 100,—
		Comm. wilde flora.	„ 50,—
		Comm. sociologie	„ 50,—
		Ivon.	„ 100,—
		Herb. en bibl.	„ 250,—
		Bijschrijven	„ 125,—
			f 800,—
Vrije Fonds.			
Achterst. contr.	*f* 1200,—	Recueil	*f* 4500,—
Interest	„ 300,—	Kr. Archief	„ 3000,—
Contributie	„ 6000,—	Herb. en bibl.	„ 500,—
Verkoop	„ 300,—	Onkosten	„ 350,—
Bijdr. Labor.	„ 1350,—	Vergaderingen	„ 150,—
		Comm. v. Physiologie	„ 100,—
		Comm. v. Phytopath.	„ 50,—
		Flora Neerlandica	„ 100,—
		Centr. Bur. Schimmelc.	„ 150,—
		Station den Helder	„ 100,—
		Contactcommissie	„ 50,—
		Nat. en Gen. Congres	„ 5,—
		Ned. Phytopath. Ver.	„ 5,—
		Onvoorzien	„ 90,—
	f 9150,—		*f* 9150,—

VERSLAGEN OVER HET JAAR 1947.

JAARVERSLAG van de eerste secretaris over 1947.

In het jaar 1947 is het leven van onze vereniging weer vrijwel volgens normale banen verlopen. De grote achterstand met onze tijdschriften echter kon door de moeilijkheden in het drukkerijbedrijf nog niet worden ingehaald.

Het Gedenkboek ter gelegenheid van het 100-jarig bestaan der Vereniging (op 15 Augustus 1945) door WACHTER samengesteld, kwam in dit jaar van de pers als deel 55 van het Nederlandsch Kruidkundig Archief, enige maanden later gevolgd door deel 54, bevattende de verslagen en mededelingen over het jaar 1943, maar met de ledenlijst en andere huishoudelijke gegevens van 1947.

De eveneens als jubileumsuitgave bedoelde Flora Neerlandica is ook dit jaar nog niet kunnen verschijnen. Wel zijn de werkzaamheden daarvoor thans zo ver gevorderd, dat het gereedkomen van een eerste deeltje in begin 1948 nu wel verzekerd schijnt.

Van het Recueil des Travaux botaniques néerlandais zal ook pas in 1948 weer een deel kunnen worden verzonden.

Het bestuur vergaderde twee maal in pleno en bovendien nog twee malen met de voorzitters en secretarissen van de permanente commissies ter vaststelling van data voor algemene en commissievergaderingen, om een zo gunstig mogelijke verdeling en combinatie van deze te verkrijgen.

Ledenvergaderingen: Op de jaarvergadering van 9 Februari 1947 werden de nieuwe statuten definitief vastgesteld. Na de wijziging van September 1946, waarbij twee nieuwe commissies, die voor de Plantenphysiologie en die voor de Plantensystematiek en -geografie waren ingesteld, werd nu in een aanvullende statutenwijziging een Archivaris toegevoegd aan de Commissie voor Bibliotheek en Herbarium, aan de Commissie voor de Phytopathologie werd toegestaan contribuanten op te nemen en de reeds lang aangekondigde contributieverhoging doorgevoerd.

In de commissies b—d, waar dit toegelaten is, werden de aftredende leden herkozen. Als archivaris werd Dr S. J. VAN OOSTSTROOM benoemd, nadat een wijziging van de Statuten dit mogelijk gemaakt had.

Aan de subcommissie voor het Zuiderzee-onderzoek werd D. PIET toegevoegd.

In de Commissie voor de Bescherming van de Wilde Flora werd J. G. SLOFF vervangen door Dr Ir W. H. DIEMONT, in die voor Biosociologie de aftredenden Dr Ir W. FEEKES, Dr F. P. JONKER en Dr V. WESTHOFF door Dr M. F. MÖRZER BRUYNS, Mr Dr F. FLOR-

SCHÜTZ en Ir J. VLIEGER. In de commissie voor de phytopathologie werd onder toepassing van het vernieuwde Statutenartikel 23 Dr J. W. M. ROODENBURG herkozen.

Het bestuur werd aangevuld, doordat op de vacante plaats van ondervoorzitter Dr LANJOUW en op die van 1e secretaris, vrij gekomen door het aftreden om gezondheidsredenen van Dr S. J. VAN OOSTSTROOM, Dr J. HEIMANS werden benoemd.

Op de morgenvergadering spraken Dr P. VAN DER LEEDEN, voorzitter van het verbond van Wetenschappelijke onderzoekers, over doel en betekenis van deze vereniging, Dr T. H. THUNG over Electronenmicroscopie en Virusonderzoek en Dr V. WESTHOFF over het associatiebegrip in geografisch verband.

De Zomervergadering werd gehouden op 11 Juli 's avonds in de Cantine te Emmeloord in de Noordoostpolder. Er was een zeer grote opkomst van onze leden, voor wie 's avonds Dr Ir A. J. ZUUR en Dr W. FEEKES spraken resp. over het werk van de Afdeling Onderzoek van de Noordoostpolder en over de ontwikkeling van de wilde begroeiing in de N.O.Polder. De deelnemers werden voor de nacht ondergebracht in door het bestuur van de N.O.polderwerken beschikbaar gestelde barakken en maakten op Zaterdag 12 Juli een door allen wel zeer geapprecieerde excursie per autobus en per vaartuig door de nieuwe polder onder leiding van de HH. Ir ZUUR en D. BAKKER. Een kleine groep leden bleef in Zwolle over, om de volgende dag, Zondag 13 Juli, een excursie te maken onder auspiciën van de Commissie voor Biosociologie (Ir SISSINGH en A. C. BOER). Deze weinige leden hebben bijzonder genoten van het prachtige landschap en de interessante Bromion-vegetaties op oude rivierduintjes bij Zalk en bij Junne (Ommen).

De herfstvergadering had plaats in Utrecht op 25 October 1947. Hoofdschotel van de avond was de film „Les champignons prédateurs" vervaardigd door de heren COMANDON en FONBRUNE van het Instituut Pasteur te Parijs. Dr A. J. P. OORT gaf niet alleen een inleiding en verklaring bij deze film over Nematodenvangende schimmels, maar kon ons ook aan levende objecten onder het microscoop laten zien hoe de aaltjes door de schimmels (*Arthrobotrys*) gevangen en verteerd werden. Voor deze vergadering was introductie toegestaan voor leden van de Nederl. Mycologische Vereniging en van de Ned. Plantenziektenkundige Vereniging.

Behalve voor deze drie algemene vergaderingen zijn onze leden in dit jaar nog door vijf onzer commissies ieder voor twee of drie vergaderingen resp. excursies geconvoceerd.

Uit de afzonderlijke verslagen dier commissies blijkt wat er op al die vergaderingen en excursies is geboden en genoten.

De vereniging werd vertegenwoordigd door de 1e secretaris bij een bijeenkomst te Utrecht ter voorbereiding van de Stichting voor Wetenschappelijk Duinonderzoek en door de voorzitter van onze Commissie voor Bescherming van de wilde Flora bij de vergadering van de Contactcommissie voor Natuur- en Landschapsbescherming.

Het contact met onze buitenlandse leden, corresponderende leden en ruilconnecties kon dit jaar wel grotendeels, maar nog niet geheel worden hervat.

In het jaar 1947 bereikte ons ledenaantal het ronde cijfer 500.

Drie leden werden ons door de dood ontnomen.

Fried van der Wouw overleed op de jeugdige leeftijd van 25 jaar als biol. cand., assistent van Prof. Koningsberger en leraar aan het St Bonifacius-Lyceum te Utrecht.

Dr J. J. Smith, die op 79-jarige leeftijd overleed (29 Juni 1867—14 Januari 1947) heeft zich een wereldnaam verworven door zijn werken over de Orchideeën van het Maleise gebied, speciaal die van Java en van Nieuw-Guinea. Talloze nieuwe soorten dragen zijn naam als auteur. Van 1891—1924 werkte Smith in de Plantentuin te Buitenzorg, laatstelijk als hoofd van het Herbarium en waarnemend directeur van 's Rijks Plantentuin. Na zijn terugkeer in Nederland heeft hij in Oegstgeest wonend nog een enorm materiaal bewerkt, waarvan een belangrijk deel nog posthuum gepubliceerd moet worden. Smith was autodidact, bezat zelfs niet het einddiploma H.B.S. De titel Dr honoris causa verleende hem de Utrechtse Universiteit in 1910.

De 20e September 1947 overleed Mej. Prof. Dr Jantina Tammes in de ouderdom van 76 jaar.

Tine Tammes is in 1871 in Groningen geboren en heeft ook haar opleiding in Groningen genoten, waar zij onderwijzeres en, na het behalen van de acte K IV, lerares aan de Rijks H.B.S. 5 j. c. werd. Behalve in Groningen bij Prof. Moll heeft Tine Tammes korte tijd in Amsterdam bij Hugo de Vries gestudeerd. In 1911 werd zij benoemd als conservator voor Botanie in Groningen en, nadat zij in 1911 honoris causa tot doctor in de Plant- en Dierkunde was gepromoveerd, volgde in 1919 de benoeming tot hoogleraar in de voor haar gestichte leerstoel in Genetica. Haar belangrijkste onderzoekingen zijn die over de variabiliteits- en erfelijkheidsverschijnselen en de veredeling van het vlas. Een eerste omvangrijke publicatie over dit onderwerp verscheen in het Recueil van 1911.

Voor onze Vereniging heeft Mej. Tammes zich grote verdienste verworven als secretaresse van de redactie voor het Recueil van de splitsing der tijdschriftredacties in 1918 tot 1923, later nog een paar jaar (1928 en 1929) als voorzitster van die commissie. J. Heimans.

VERSLAG van de Commissie van Redactie van het Recueil des Travaux botaniques néerlandais over 1944 tot en met 1947.

In aansluiting aan het verslag over 1943, afgedrukt in het Nederl. Kruidkundig Archief, deel 54 (1947) pag. 4, kan het volgende worden medegedeeld.

In de loop van 1944 bleek, dat de Duitse autoriteiten geen genoegen wilden nemen met de in het Duits gestelde „Zusammenfassungen" van de nog af te drukken artikelen. Het was dus nu onmogelijk geworden deel XL af te drukken. Intussen waren van het artikel van R. C. Bakhuizen van den Brink 10 exemplaren clandestien afgedrukt waardoor het mogelijk werd, dat deze op 17 Mei 1943 te Utrecht kon promoveren tot doctor in de wis- en natuurkunde. Een Nederlandse samenvatting van zijn publicatie diende daarbij als schijn-dissertatie; de tien boven bedoelde exemplaren waren ter beschikking gesteld van de aanwezige leden der Faculteit en werden na afloop der promotie de jonge doctor ter hand gesteld.

Tengevolge van storingen in de drukkerij en gebrek aan papier kon deel XL pas in Dec. 1946 verschijnen. Het is 559 pagina's groot en bevat de volgende artikelen:

R. C. Bakhuizen van den Brink Jr, A contribution to the knowledge of the Melastomataceae occurring in the Malay Archipelago especially in the Netherlands East Indies (dissertatie Utrecht); G. L. Funke, Observations on the Flowering Periodicity; A. Quispel, The Mutual Relations between Algae and Fungi in Lichens (dissertatie Groningen); Maartje A. Goedewaagen, Investigations sur les tourbières néerlandaises. De drukker is al geruime tijd bezig met het zetten van kopie voor deel XLI. Het is te verwachten dat nog in Januari 1948 een eerste aflevering van dat deel zal kunnen verschijnen.

Baarn, 31 Dec. 1947.

De Secretaris,
A. Pulle.

VERSLAG der Commissie van Redactie voor het Nederlandsch Kruidkundig Archief over 1947.

De grote achterstand, die in de publicatie van de verslagen onzer vereniging in de oorlog is ontstaan, werd ook dit jaar niet ingehaald, al verschenen dan twee delen van het Archief. In Mei zag eindelijk het Gedenkboek – deel 55, dat in 1945 had moeten verschijnen – het licht. Helaas heeft wijlen Dr W. H. Wachter, die het heeft samengesteld en een eeuw geschiedenis der Botanische Vereniging met grote liefde erin beschreven heeft, de uitgifte niet meer mogen beleven. In het najaar verscheen deel 54, eveneens nog door Wachter samengesteld. Het bevat de verslagen over 1943 en naast enkele korte floristische mededelingen het proefschrift van Mej. Andreas, dat afzonderlijk reeds in Februari 1946 verschenen was. Daar de eisen van het verenigingsleven de publicatie van de tegenwoordige toestand der vereniging dringend vroegen, werd de ledenlijst van 1947 opgenomen. Het gevolg is echter, dat de samenstelling der commissies enz. over verscheidene jaren nooit gepubliceerd is.

Het papier der beide verschenen delen was gelukkig weer van goede kwaliteit.

De commissie besloot om voortaan bij in het Nederlands geschreven wetenschappelijke artikelen een Engelse samenvatting verplicht te stellen.

Nijmegen, 31 Dec. 1947. De Secretaris,
J. H. Kern.

VERSLAG van de Commissie voor de Bibliotheek en het Herbarium over 1947.

Door drie leden van de Vereniging werd dit jaar het herbarium aan het Stamherbarium afgestaan: Prof. Dr Th. Weevers bood zijn collectie, bestaande uit 1106 Phanerogamae en Cryptogamae, aan; Dr W. C. de Leeuw schonk zijn type-verzameling van 932 nummers en tenslotte Dr F. W. T. Hunger zijn herbarium van 810 nummers. Voorts stond de Heer Johan Jansen 245 Pteridophyten af en de Heer J. J. Barkman 1 mos. Het herbarium werd dus dit jaar met 3094 nummers verrijkt.

Uit de collecties van de Vereniging werden dit jaar zendingen uitgeleend aan de volgende personen: E. Agsteribbe (91 Musci), Olaf Anderson, Lund (2 Fungi), Mej. Dr Ch. H. Andreas (17 Coniferae, 254 Nymphaeaceae en Gentianaceae), W. Margadant (90 Musci), Dr O. Almborn, Lund (123 Lichenes), Dr H. R. Hoogenraad (71 Compositae), Prof. Dr van der Wijk (184 Musci), J. H. Kern (1 Cyperacee). Uit vorige jaren zijn nog ruim 2000 planten uitgeleend aan verschillende personen.

De bibliotheek werd door 19 bezoekers bezocht, terwijl 244 werken werden uitgeleend.

Als bijlage bij dit verslag is opgenomen een lijst van aanwinsten 1). Buiten hetgeen door ruilverkeer werd verkregen, ontving de bibliotheek door schenking een aantal proefschriften en overdrukken: Dr H. C. Bels-Koning, Dr W. Beijerinck, Prof. Dr R. Florin, Stockholm (16), Dr G. J. M. A. Gorter (4), Prof. Dr L. A. Gosse-

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1) Zie noot op pag. 6. Red.

LIN, Montreal (2), Prof. Dr J. HEIMANS (3), Dr Ir A. W. KLOOS Jr (2), Dr J. LANJOUW (2), Dr R. A. MAAS GEESTERANUS, Dr M. F. MÖRZER BRUIJNS, Dr A. J. P. OORT (3), Dr S. J. VAN OOSTSTROOM (14), Dr J. VAN OVERBEEK (5), Dr M. H. VAN RAALTE, E. VAN ROMPAEY, Kapellen (2), Dr CH. G. T. P. SCHNELLEN, Prof. Dr M. J. SIRKS (8), Ir J. L. VAN SOEST (15), Dr C. G. G. J. VAN STEENIS (18), Dr P. VERMEULEN, Dr E. C. WASSINK, Dr J. WESTENBERG, Dr V. WESTHOFF (2). Voorts van de volgende instituten: A.N.W.B. (2), British Museum (22); Contactcommissie voor Natuur- en Landschapsbescherming (2); Geobotanisches Forschungsinstitut Rübel (4); Institut für Systematische Botanik, Graz (15); Instituut voor Plantenveredeling, Wageningen (35); Instituut voor veredeling van tuinbouwgewassen, Wageningen (4); Laboratorium voor Technische Physica, Delft; Ned. Natuurhistorische Vereeniging; Pioneer Hi. Bred Corn Comp., Des Moines, Iowa.

Door aankoop werd verkregen: DELARBRE, Flore d'Auvergne 2 dln, 1800.

's Gravenhage, 1 Januari 1948.

De Secretaris,
J. L. VAN SOEST.

VERSLAG van de Commissie voor het Floristisch Onderzoek van Nederland over 1947.

Ook dit jaar werden 2 vergaderingen gehouden, die zich in een zeer druk bezoek mochten verheugen. De voornaamste mededelingen zullen, naar wij hopen, nog eens in een Kruidkundig Archief geplaatst worden.

De zomerexcursie werd onder leiding van Dr Ir A. W. KLOOS in de omgeving van Coevorden gehouden. De commissie stelt voor, in 1948 een zomerexcursie te houden in de omgeving van Oost-Voorne gedurende de laatste week van Juli.

De Secretaris,
P. JANSEN.

VERSLAG van de excursie der Kon. Ned. Bot. Ver. te Coevorden en omgeving op (21) 23—27 (29) Augustus 1947.

Ter voorbereiding van deze excursie ging ondergetekende na een weinig bemoedigende correspondentie met diverse Coevordense hotels, op 5—7 Juni eens ter plaatse poolshoogte nemen en kwam terecht in een feestvierende stad en in het boordevol hotel Holman, het enige dat ons in Augustus zou kunnen herbergen. Maar voor mij was er nu geen plaats en ik werd uitbesteed bij Dr BEZOEN, waar ik beide nachten mocht logeren en buitengewoon hartelijke gastvrijheid genoot. Het wonderlijke toeval deed zich voor, dat ik juist terecht gekomen was aan het adres, waar de beide Bianchi's, die zich ook als deelnemers aan de excursie hadden opgegeven, hun intrek zouden nemen. Weinig vermoedde ik echter, dat mijn bevindingen in het hotel een voorbode zouden zijn van wat ons in Augustus te wachten zou staan, een gebeuren, dat z'n invloed op onze excursie had en haar een onrustig, rommelig karakter gaf. De samenkomst was bepaald op 22 Augustus. Maar reeds de 21ste begon Sloff met trein-notities, afgewisseld met volledige inventarisaties in de hokken. L7. **51** 44, **53** 42, 43, **61** 13, 14, 21, 22, **62** 11, 12, 21, 22, **63** 11, 12, 21, 22, wat hij de volgende dag voortzette in L7. **25** 24, 42, 43, **26** 13, **35** 31, 33, **44** 22, 23, 43, **54** 21, 23, 32, 33, 34, **61** 13, 14, 21 en **64** 11. — P. Jansen, Kruseman en Kloos brachten 's morgens een bezoek aan enkele van ouds bekende terreinen in Deventer, waar de adventiefflora weliswaar nog niet rijk was, maar toch blijkbaar herstellende. Onder meer werden waargenomen: *Eragrostis minor* en *abyssinica*, *Glaucium corniculatum* var. *tricolor*, *Chenopodium album pseudopulifolium*, *Setaria viridis*, *Solanum nigrum chlorocarpum* en *Hirschfeldia incana* var. *incana*. f. *leiocarpa*. De trein bracht ons naar Coevorden, waar wij aan het station door de Bruin, Joh. Jansen, Sloff en v. d. Wijk werden verwelkomd met de blijde tijding, dat de excursie in het hotel niet verwacht werd. De hotelhouder beweerde sedert onze besprekingen in Juni niets meer van mij vernomen te hebben, hoewel ik, zoals afgesproken was, einde Juli hem uitvoerig geschreven had. – Het was natuurlijk mijn fout, dat ik geen bevestiging van de ontvangst van mijn brief had gevraagd. — Er was een geweldig huwelijksfeest in het hotel, dat stampvol was met bruiloftsgasten. Wij konden daarom de beide eerste nachten daar niet logeren en werden eerst in twee, later in drie groepen uitbesteed. Inmiddels waren Brand, v. Ooststroom, van der Wijk, Vlieger en Heimans gekomen en werden 's avonds v. Soest en Westhoff nog verwacht. Na het diner vertrok de grootste groep naar hotel de Boer in Dalen, deels in de auto van de zaak, deels met die van Vlieger; het waren Brand, de Bruin, Heimans, P. Jansen, Kruseman, v. Ooststroom, Sloff, Vlieger en v. d. Wijk, terwijl Joh. Jansen en Kloos in Coevorden bleven. Spoedig voegde zich Westhoff bij ons en gezamenlijk haalden wij v. Soest van de laatste trein, na de avond o.a. benut te hebben om ons ten huize van Dr Bezoen met vader en zoon Bianchi in verbinding te stellen. Wij kregen onderdak in een klein kroegje met primitieve, maar keurig nette logeergelegenheid. 's Morgens zouden wij gezamenlijk in Hotel Holman ontbijten, maar toen het Dalense gezeldingen in het hotel een voorbode zou zijn van wat ons in Augustus schap door de goede zorgen van Vlieger in twee groepen aankwam, bleken die reeds een voortreffelijk ontbijt genoten te hebben. Zij waren vol lof over hun logies, maar brachten het bericht mee, dat twee van de gasten 's avonds niet terug mochten komen. Na veel gezanik kwamen Brand en P. Jansen 's avonds samen met Stomps en Weevers, die 's middags arriveerden, in hotel Wely uitstekend terecht.

's Morgens maakten wij allen gezamenlijk, na een half uurtje oponthoud aan het Douane-kantoor, waar wij ten slotte een 4-tal vergunningen op naam kregen om in de verboden strook te botaniseren, op uitdrukkelijke voorwaarde, dat wij niet met Duitsers zouden spreken, een wandeling ten Z.O. van de stad, langs het kanaal van Oud Picardië tot aan de grens en van daar door het bouwland noordwaarts tot de Schoonebeker straatweg en zo naar Coevorden terug. Daar wachtte ons een nieuwe verrassing. Er was niet op de lunch gerekend. Rond het biljart werden enkele sneedjes brood en wat koffie geserveerd, een naburige fruitwinkel werd leeg gekocht, eerst van goede Clapsfavorite, later onrijpe jutteperen, ook enige ontbijt- en andere koeken doken op; intussen werd met de hotelier geconfereerd, die 's avonds een diner en vanaf morgen na de bruiloftsdrukte, een goede verzorging beloofde. Kort daarop deed zich een incident voor. Kruseman kwam binnenvallen met het bericht, dat we 's avonds allen in Dalen terecht konden. Hij was dit inmiddels gaan afspreken in overleg met een aantal leden van het gezelschap en in de mening, dat ook ik van zijn missie wist en er mee accoord ging. Toen dit echter niet het geval bleek en daar ik juist met de huisbaas tot overeenstemming gekomen was, werd Dalen weer afgezegd en was hiermede het incident gesloten. In drie groepen gingen wij toen de petroleumvelden verkennen. De eerste groep fietsers, Bianchi Jr Heimans, Joh. Jansen, Kruseman, v. Ooststroom en van der Wijk noteerden in L7. **27** 12 en 21, de tweede groep, Bianchi Sr, de Bruin, P. Jansen, Sloff, Weevers en Westhoff, fietste wat verder op en inventariseerde L7. **18** 34 en **28** 11, terwijl de derde groep: Brand, Kloos, v. Soest en Vlieger per auto tot aan de grens ten O. van Nieuw Schoonebeek reed en de hokjes L8 **25** 14, 21, 24, **26** 12, 13 en 14 bewerkte. Zondag 24 Aug. 's morgens door een groot gedeelte van het gezelschap een wandeling langs haven, fabriek en spoorwegterreinen, stortplaatsen en vuilnisbelt ten Z.W. van de stad gemaakt, vrijwel geheel in L7 **26** 11. De auto ging met P. Jansen, v. Soest, Stomps en Vlieger naar Gramsbergen, waar westelijk van deze plaats de hokjes L7 **25** 11, 12, 13 en 31 opgenomen werden. De groep de Bruin, Heimans en Joh. Jansen fietste naar Holthone en inventariseerde L7 **25** 14 en 41. De tweede groep fietsers, Brand, Bianchi Sr, Kruseman, Sloff, Weevers en Westhoff namen in dezelfde richting L7 **25** 23 voor hun rekening. 's Middags ging, ondanks de sterke wind, een grote groep fietsers naar de plaats waar de Vecht ons land binnenvalt. Inventarisaties van de hokken L7 **25** 42, 43, **35** 22 en 24 werden gemaakt en een rups van de Koninginnepage, die in **35** 24 op *Pimpinella saxifraga* huisde, werd naar Amsterdam geëvacueerd.

Maandag 25 Aug. 's morgens fietsen Bianchi, de Bruin, Heimans, Joh. Jansen, Kruseman, v. Ooststroom, Sloff, v. Soest, Weevers en Westhoff naar het N.-Westen, verdelen zich in groepen en vullen excursielijsten in voor de hokken K7 **65** 33, L7 **14** 12, 14, 21, 22, 32, 34 en **24** 12, terwijl de auto met Vlieger, P. Jansen, Kloos, Stomps en v. d. Wijk nog verder westelijk naar het Hollandse veld gaat, waar een stevige wandeling door de hokken L7 **13** 14, 34 en 24 wordt gemaakt. 's Middags begint het gezelschap reeds aanmerkelijk te dunnen en gaat de groep Brand, de Bruin, Joh. Jansen, P. Jansen, Kloos en v. Ooststroom de hokken L7 **15** 42 en 44 bewerken.

Dinsdag 26 Aug. maken Bianchi, de Bruin, Heimans, Joh. Jansen, v. Ooststroom, Sloff en Stomps een dagtocht, door met de trein naar Gramsbergen te gaan en van daaruit te voet de hokken L7 **35** 12, 14, 21, 23, 24 en 42 te bewerken. In **35** 21 worden coloradokevers in een akker gesignaleerd. P. Jansen en Kloos gaan 's morgens op de fiets naar het Noorden tot aan de Oosterhesseler brug over de Hoogeveense vaart, hokkende in K7 **65** 22 en 24, lunchen dan in Dalen om vervolgens in K7 **66** 33, 34, 43 en 44 noterende, langs de spoorlijn over Dalerveen naar Coevorden terug te keren.

Woensdag 27 Aug. 's morgens maken de overblijvenden, Bianchi, de Bruin, Heimans, Joh. Jansen, P. Jansen, Kloos, Sloff en v. Ooststroom nog een tochtje naar L7 **16** 31. Nu voegt zich v. d. Kloot nog bij het gezelschap en maakt met Bianchi en Sloff, nadat zij de overigen uitgeleide hebben gedaan, nog een autotocht naar L7 **18** 12 en L8 **15** 13, 31 en 41, waarna Sloff alleen nog aantekeningen maakt in L7 **16** 32, 33, 34, 41, 42, **17** 31 en 32. Donderdag 28 Aug. zet hij dit nog voort in L7 **34** 24, 42, 43, 44, **44** 21, 34 en 41 en Vrijdag 29 Aug. in L7 **44** 32, **53** 24, 42, 44 en **63** 22. —

In totaal werden voor 80 hokken excursielijsten ingevuld, terwijl bovendien lijstjes met losse opgaven aanwezig zijn uit 22 andere. De lijst van glossen op plantenbussen kan worden aangevuld met de geestigheid van een jeugdige Drent: „Die vent loopt nou nog met een gasmasker".

In de hier volgende lijst van waargenomen soorten is achter de naam aangegeven het aantal malen, dat zij genoteerd is; indien dit aantal boven de 25 ligt (meestal belangrijk daarboven) is zij als algemeen (*a*) aangegeven. Als van een soort op de excursie herbariummateriaal is verzameld, is tussen [ ] aangegeven door wie dit is geschied.

B. betekent dan Dr J. Brand te Doesburg, H. = Prof. Dr J. Heimans te Amsterdam, Joh. J. = Joh. Jansen te Malden †, herb. nu in Leiden, P. J. = Dr P. Jansen te Amsterdam, K. = Kloos te Dordrecht, O. = Dr S. J. van Ooststroom te Leiden, S. = Ir J. L. van Soest te 's Gravenhage, V. = Ir J. Vlieger te Leeuwarden en W. = Dr V. Westhoff te Driebergen.

In het blad L8 was nog nooit genoteerd. Als eerste plant in dit kaartblad werd aangeschrapt: *Polygonum aviculare*, die, voorzover uit de 8 nu van dit blad aanwezige inventarisaties blijkt, wel typerend is voor de povere flora van die streken. In het blad K7 zijn slechts 6 hokjes bewerkt. De daar gevonden planten zijn alleen afzonderlijk vermeld, als zij op de L-bladen niet genoteerd waren op deze excursie.

Acer, *Pseud.* (4) Ach, *m* (a) ook herhaaldelijk roodbloemig, *p* (a). Acor (a). Aeg. (22). Aeth. (6). Agrostis *a* (a), *c* (a) *v* (a)Air *c* (a), *f* (9). Aj *r* (2). Alch *v* (1). Alis *n* (1), *P* (a). Aln *g* (a), *i* (1). Alop *a* (3), *g* (12), *p* (4). Amar *r* (2). Ambr *a* (1) Amelanchier canadense? (3). Ammo *a* (1). Andr (1) in L8. Ang (a). Anthem *ar* (1). Antho *o* (a), *P* (11). Anthr *s* (21). Ape *S* (19). Arrh (6). Art *v* (a). Aspl *R—m* (1). Athy *f—f* (14) [O.]. Atri *lat* (16), *p* (24) [O. grove vorm met grote en kleine vruchtkelkbladen]. Av *fa* (1), *prae* (6), *sativa* (9).

Bat *het* (1). Bel (a). Beru (2) Betu (a). Bid *c* (23) ook vaak f. *radians* [O.], *connatus* (19) [B.O.S.V.W.], *melanocarpus* (19) [B.O.S.], *t* (a). Ble (2). Bras *o* (5). Bro *i* (2), *m* (24), *r* (1). But (12).

Calama *la* (19) ook var. *angustifolia* [P.J.]. Cale *o* (2). Calli (4) [W.] *s* (1), *v* (1) [Joh. J.]. Callu (a). Calt (12). Camp *rot* (21). Caps (a). Carda *p* (11). Cardu *cr* (3). Care *ac . . a* (4), *ar* (9), *disti* (3), *hi* (15), *lepo* (8), *mu* (1), *nemorosa* (4), *panicu* (2), *pi* (3), *Ps* (2), *re* (1), *ro* (5), *stric* (1), *vulg* (6). Centa *Cy* (a), *decipiens* (4) [S]., *diluvialis* (1) [S], *J* (19), *microptilon* (3) [S], *pratensis* (2) [S.]. Ceras *ar* (13), *s* (4), *tr* (a). Cerat *d* (4). Chae *t* (8). Chel (2). Chen *a* (a), *Berlandieri* (1) [O.], *b—h* (1), *p* (4), *r* (1). Chrysa *i* (20), *L* (20) [O. abnormaal ex. zonder lintbloemen], *s* (3). Cicu (22). Cin *p* (1). Cirsi *ar* (a) ook witbloemig [O.], *l* (19), *p* (23). Com (17). Conva *maj* (2). Convo *a* (3), *se* (22). Corr (1). Coryd *cl* (17). Coryl *a* (2). Coryn *c* (12). Crat *m* (20), *o* (3) [O]. Crep *b* (1), *v* (15). Cus *eu* (5) [O.]. Cynod *D* (1). Cynos *c* (14).

Dac (a). Dau (9). Dian *d* (15) [S]. Dipl. *t* (1). Dra *v* (1). Dro *i* (2), *r* (4).

Elo (14). Epil *a* (a). *h* (12), *m* (3), *pal* (9) [O.], *par* (2), *r* (1) *v* (2). Epip *l* (3). Eq *a* (a), *l* (16), *littorale* (2) [W.] *p* (10) [O.] ook f. *polystachyum* [O.]. Eric *T* (a), Erig *c* (16). Erio *p* (5), *v* (1 in K.7). Erod *c* (9) [O.]. Erys *Ch* (5), *h* (1). Eupa (1). Eupho *H* (3), *Pep* (2). Euphr *Od* (5), nemorosa (3), stricta (23) [W.].

Fes *a* (7), *e* (a) [P. J.], *g* (1), *o* (a), *rub* (a) Frax (22). Fu *o* (1).

Galeops *b* (4), *T* (a), *v* (2). Galins *p* (a). Galin *Ap* (13), *M* (2), *p* (a), *sax* (6), *u* (9), *v* (19). Gent *P* (2). Ger *m* (3), *pu* (2). Geu *u* (10). Gle (a). Gly *d* (2) [O.], *f* (a), *s* (a). Gna *s* (1 in K7), *u* (a).

Hed (7). Heleo *a* (7), *p* (9). Helianthus (1) [O. S. K.]. Hera (18). Hern *g* (7) [S.]. Hiera *laev* (a, ook ssp. *rigidus*), *Pi* (a) [S], *u* (7). Holc *l* (a), *m* (a). Hor *sativum* (1). Hott (8). Hu (a). Hydroch (a). Hydroco (a). Hyo (1). Hype *hu* (2), *pe* (a), *q* (8), *t* (2) Hypo *r* (a) ssp. *erecta v. S.* (2) [S].

Ile (4). In *b* (2). Ir *ps* (a).

Ja *m* (12). Junc *bu* (a), *cong* (2), *e* (a), *f* (2) [H.V.W.], *l* (9), *o* (1), *pratensis* = *l* × *sy* (1) [O.], *su* (2, alleen in L8), *sy* (4), *tenu* (5). Juni (9).

Lac *sativa* (1) [O.]. Lami *al* (23), *p* (4). Lamp (7). Lap *sp* (8), *notha* (10), *t* (1) [K.O.]. Lathy *pa* (1), *pr* (2). Leer (3) [P.J. H.W.]. Lem *g* (1), *m* (a), *p* (17), *t* (6). Leont *a* (a). Lepid *densifl* (1) [H.], *neglec* (1) [H.] *rud* (2). Limn (7). Lina *m* (1), *v* (a) [O. *pelorie*]. Linu *usit* (1). Lol *m* (15), *p* (24). Lon *P* (15). Lot *c* (19) [O], *u* (a). Luz *c* (3), *mu* (1). Lychn *d* (a), *F* (21), *ves* (13), *d* × *ves* (4) [Joh. J. O.]. Lycopo *cl* (1) Lycopu (24). Lys *Nu* (15), *t* (9), *v* (a). Lyt *S* (a). **M**aj (5). Malv *m* (1), *v* (1). Matr *Ch* (7), *d* (12). Med *f* (1), *l* (3). Melam *p* (1), Melil *ar* (1). Ment *aq* (16), *ar* (a), *aq* × *ar* (23) [O.], *velutina* (3). Meny (3). Moehr (6). Mol (a) subsp. *litoralis* [P. J.]. Mont *m* (1). Myoso *c* (1), *h* (1 in L.8), *i* (5), *p* (a). Myric *G* (1).

Nardu (6). Narth (1). Nast *am* (22), *p* (24), *s* (2). Nu (a). Ny (15).

Oena *Ph* (14). Oeno *b* (6). Onon *s* (11) [O.]. Ornithog *u* (1). Ornithop *p* (1 en 1 in K.7). Osm (8). Ox *a* (1), *s* (7).

Pan *C—G* (23), *laevifolium* (2) [P. J.], *l* (6), *miliaceum* (1). Ped *p* (1). Pep (1) Peta *o* (1). Phalar *a* (22). Phl *p* (a). Phr (a). Pim *m* (1), *S* (14). Pinu *Pin* (1), *sy* (17). Plan *l* (a), *m* (a). Poa *a* (a), *n* (4), *pr* (a), *se* (7) [O.] *t* (10). Polygona *m* (8), Polygonu *am* (a) *av* (a), *C* (a), *condensatum* (3) [O.], *D* (12), *H* (a), *lap* (a) *min* (12) [O.], *mit* (11) [O.] f. *albiflorus* [O.], *n* (6), *Pe* (a), *H* × *min* (1) [O.]. Polypod (7). Polys *F—m* (6) *s—dil* (15), *s—eusp.* (19). Pop *canad* (2), *monilifera* (1), *n* (4), *t* (10). Pota *cr* (1), *l* (13), *n* (21), *pec* (1), *per* (6). Potent *ans* (a), *arg* (1), *pr* (4), *rep* (3), *T* (a). Prune (22). Prunu *cerasus* (3), *Pa* (4), *serot* (2), *sp* (18). Pt (4).

Qu *R* (a), *s* (1), *R* × *s* (1).

Ran *ac* (a), *b* (2), *Fl* (a), *L* (2), *r* (a), *sce* (3). Raphanu *r* (10), *s* (2). Rha *c* (1) [O.], *F* (a). Rhina *ma* (3) ook f. *serotina* [B.], *mi* (4). Rhynch *a* (3), *f* (1 in K.7). Rib *G* (1), *n* (7), *r* (1) [B.]. Rob (9). Ros *agrestis* (2) [B. Joh. J. O. S.], *ca* (13), *du* (2), *ru* (1). Rubus *spec* (22), *affinis* (3) [S], *fissus* (4), *gratus* (1), *Id* (15), *nemorosus* (7), *plicatus* (13). Rum *Ac . . . sa* (a), *Ac . . . la* (a), *cr. Hyd* (a), *o* (a), *sa* (1).

Sagin *n* (1), *p* (16). Sagit (a). Salix *ac* (4), *al* (16), *amy* (20) [O.], *au* (a) [O.], *ca* (1), *ci* (a) [O.], *au* × *ci* (2) [O.], *f* (3) [O.], *al* × *f* (1) [O.], *am* × *f* (1) [O. ook m. *stipitata*], *pe* (2) [O.], *pu* (4), *re* (a) [O.], *vim* (15) [O.] var *angustifolius* [O.], *ca* × *vim* (1) [S.], *ci* × *vim* (1) [O.]. Samb *n* (a, ook herhaaldelijk var. *laciniata*). Sang *m* (1), *o* (4). Sar (a), Scir *cae* (1 in K7), *l* (8), *se* (2), *sy* (12). Sclera *a* (6), *p* (4). Scro *no* (12). Scut *g* (a). Secale (4). Sed *ac* (3), *B* (2), *p* (18), *r* (2). Senec *a* (11), *J* (2), *p* (1), *sy* (19), *vi* (4), *vu* (a). Set *vi* (7). Sin *al* (1), *ar* (8). Sis *A* (1), *o* (a), *S* (1). Siu (12). Sola *D* (a), *n* (a), *tuberosum* (6). Soli *canadense* (1), *serotina* (3) [O.], *v* (5). Son *ar* (8), *as* (12), *o* (6). Sor *a* (a). Sparg *r* (18, vermoedelijk steeds ssp. *polyedrum*), *s* (8). Spergula *a* (a) Spergularia *r* (10). Spirae *U* (a). Stach *ar* (2), *p* (a). Stel *gl* (16), *gr* (22), *m* (a), *u* (2). Stra (15), Suc (a). Sym *o* (22).

Tan (a). Tar (a), *vulgaris* (5), *parvuliceps* (4) [B. S.]. Teu *sc* (2), Tha *fla* (4). Thl *ar* (3). Thr (9). Thym *ang.* (8), *Cham* (3). Thys (19). Tor *A* (8). Trag *pr* (3). Trif *ar* (3), *h* (10), *mi* (11), *pra* (a), *rep* (a). Trigl *p* (6). Trit *r* (a), *sativum* (1). Tus (6). Typha *a* (14). *l* (14).

Ulm *c* (8). Ur *d* (a), *u* (10). Utr. *v* (2).

Vacci *My* (4), *V* (2). Valeriana *d* (1), *o* (24). Verba *n* (1). Vero *An* (1), *ar* (2), *Be* (1), *Ch* (7), *lo* (13) [H. O. S.], *of* (3), *sc* (5), *se* (4). Vib *O* (14). Vic *C* (a), *Faba* (1). Vio *can* (16), *pa* (14), *st* (1), *t –arv* (13) *-hort* (2) *-vulg.* (7).

Zea *Mays* (1).

Bij het inboeken van deze gegevens in de I.V.O.N.-albums bleek voor het kaartblad L7, dat niet minder dan 75 nieuwe fiches moesten worden ingelegd, wat het aantal voor dit blad bekende soorten van 593 op 669 bracht.

A. W. KLOOS Jr.

Lijst van waargenomen blad- en levermossen.

Het aantal gevonden soorten is niet groot. Bovendien zijn het practisch alleen de algemeen voorkomende soorten. De oorzaak moet naar mijn mening grotendeels toegeschreven worden aan de droge zomer, waardoor onderscheiden der soorten in het vrije veld heel moeilijk was en vele soorten niet opvielen.

De nummers hebben betrekking op kaartblad L7. De enkele van de kaartbladen L8 zijn apart aangegeven. De namen zijn genomen in overeenstemming met de lijst, zoals die in Buxbaumia no. 4 (van 1947) is verschenen.

Bladmossen.

Atrichum undulatum (= Catharinea undulata). **25**, 23; **25**, 32; **25**, 41; **26**, 14; **26**, 21; **35** 22. L8, **16**, 33. Aulacomnium androgynum. **13**, 24. Brachythecium albicans. L8, **26**, 14. Bryum argenteum. **25**, 34; **26**, 11; **35**, 22. Bryum pallescens. **26**, 12. Ceratodon purpureus. **25**, 14; **25**, 41; **26**, 11; **26**, 12; **35**, 24; L8, **26**, 14. K7, **27**, 12. Climacium dendroides. **26**, 12; **27**, 12; **35**, 11. Dicranella heteromalla. **13**, 23; **13**, 24; **16**, 33; **25**, 23; **25**, 32; **25**, 34; **25**, 41; **35**, 22. Dicranum scoparium. **13**, 23; **13**, 24; **25**, 34; **35**, 11. Dicranum rugosum (= undulatum) **13**, 24. Dicranoweisia cirrhata. **25**, 32; **25**, 41; **35**, 22. Drepanocladus exannulatus. **26**, 11. Funaria hygrometrica. **26**, 12. Grimmia pulvinata. **16**, 33. Hypnum cupressiforme. **13**, 23; **13**, 24; **16**, 33; **25**, 23; **25**, 32; **25**, 34; **25**, 41; **35**, 11; **35**, 22; **35**, 24. L8, **26**, 14. Leucobryum glaucum. **13**, 24; **25**, 23. Mnium affine. **35**, 21. Mnium hornum. **13**, 23; **13**, 24; **25**, 32; **25**, 41. Physcomitrium pyriforme. **26**, 21; **35**, 21; **35**, 24. Plagiothecium undulatum. **25**, 23. Pleurozium Schreberi. **13**, 23; **13**, 24; **25**, 23; **25**, 34; **26**, 12; **35**, 11. Pohlia nutans (= Webera nutans). **13**, 23; **25**, 23; **25**, 41; **27**,12; L8 **26**, 12. Polytrichum formosum (= attenuatum). **25**, 23. L8, **25**, 21. Polytrichum commune. **13**, 23; **13**, 24; **25**, 34; **35**, 24. Polytrichum juniperinum. **16**, 33; **25**, 41; **27**, 21; **35**, 24. Polytrichum marginatum (= gracile). L8, **26**, 12. Polytrichum piliferum. **26**, 11; **26**, 12; **27**, 21; **35**,11. Pseudoscleropodium purum. **13**, 24; **25**, 23: **25**, 41; **26**, 11; **26**, 12. Rhynchostegium megapolitanum. **13**, 24. Rhytidiadelphus squarrosus. **13**, 23; **25**, 23; **25**, 41; **26**, 12; **27**, 12; **35**, 11; **35**, 21; **35**, 24. Sphagnum compactum. **13**, 23. L8, **26**, 12. Sphagnum cuspidatum. **13**, 23. Sphagnum fimbriatum. **13**, 23. Sphagnum palustre. **13**, 23. Sphagnum recurvum. **13**, 23; L8, **26**, 12. Tortula muralis. **16**, 33.

Levermossen.

Anthoceros punctatus. **26**, 21; **35**, 24. Blasia pusilla. **26**, 21; **35**, 24. Lophocolea bidentata. **13**, 24; **27**, 12. Marchantia polymorpha ♀. **26**, 12; **26**, 21; **35**, 24. Pellia epiphylla. **16**, 33; L8, **25**, 14. Riccia fluitans (= Ricciella fluitans). **25**, 23; **26**, 12.

R. v. D. WIJK.

Waargenomen Lichenen.

Cladonia impexa, Kanaaldijk Gramsbergen L7, **35**, 12. Xanthoria parietina, vrij algemeen, o.a. L7, **26**, 11, **35**, 12. X. candelaria L8, **25**, 14. Evernia prunastri. L8, **25**, 14. Parmelia sulcata en P. physodes beide L8, **25**, 14. Physcia tenella, Nieuweland, det. MAAS GEESTERANUS, ook L8, **25**, 24 enz. Ph. caesia, Nieuweland, det. MAAS GEESTERANUS.

Ir J. L. VAN SOEST.

VERSLAG van de Subcommissie voor het Zuiderzee-onderzoek over het jaar 1947.

In 1947 werd een excursie gemaakt door JANSEN, KLOOS en CROOCKEWIT langs de Westelijke oevers van de voormalige Zuiderzee alsmede in de Wieringermeer.

Het correspondentieblaadje kon door laat binnenkomen van copy dit jaar niet meer verschijnen. In 1948 zal begonnen worden met de publicatie van deel VII, waarin nog een aantal excursie-verslagen van 1946, alsmede dat van 1947 zal worden opgenomen. Tevens kwamen nog een paar andere bijdragen hiervoor binnen.

De secretaris voerde nog enige correspondentie met medewerkers, die, naar vertrouwd wordt, t.z.t. wel met aardige nieuwe bijdragen voor den dag zullen komen.

De Secretaris.
H. W. E. CROOCKEWIT.

VERSLAG van de Commissie voor de Biosociologie en het Veenonderzoek in Nederland over het jaar 1947.

In dit jaar werden wederom twee bijeenkomsten georganiseerd, nl. de 19de en 20ste Nederlandse Dagen voor Biosociologie en Palaeobotanie. Daar tegen het houden van bijeenkomsten op Zondagen van verschillende zijden bezwaren waren ingebracht, werd besloten afwisselend op Zaterdagen en Zondagen te vergaderen. De 19de bijeenkomst vond zodoende plaats op een Zaterdag, de 20ste op een Zondag.

De 19de Dag vond plaats op 17 Mei 1947 in de collegezaal van het Geologisch-mineralogisch Instituut te Utrecht. Inleidingen werden gehouden door H. T. WATERBOLK over de natuurlijke bosvegetaties in Drenthe, door Dr A. D. VOÛTE over regulerende elementen in de dierlijke samenleving, door TH. DE BOER over inundatiegrasland, door Ir P. TIDEMAN over de flora van de garrigues in de Franse Midi en door H. J. ZWART over de vegetatie van de brongebieden in de Lutte.

De 20ste Dag vond plaats op 23 November 1947 in de collegezaal van het Botanisch Laboratorium te Utrecht en werd bezocht door 39 leden en 6 introducé's. Inleidingen werden gehouden door J. BARKMAN over enige Epiphytenassociaties in Zwitserland, door Mej. A. C. STOLK over pollenanalytisch onderzoek van het Haaksbergerveen, door Drs D. BAKKER over de flora en fauna van Walcheren tijdens en na de inundatie, door Ir P. DEN DULK over de vegetatie van de voormalige blauwgraslanden van het Binnenveld bij Wageningen en door Dr V. WESTHOFF over de plantengroei van de Botshol.

Voor het eerst werd dit jaar in aansluiting bij een algemene ledenvergadering op Zondag 13 Juli 1947 een excursie gehouden. Bezocht werden het Medicagineto-Avenetum langs de IJssel in de buurt van Spoolde-Westenholte en het Festuceto-Thymetum in het Junner Koeland aan de Vecht bij Junne.

De Secretaris.

Den Dolder, 20 Dec. '47. Ir W. G. VAN DER KLOOT.

VERSLAG van de Negentiende Nederlandse Dag voor Biosociologie en Palaeobotanie, gehouden op 17 Mei 1947 in de collegezaal van het Geologisch-Mineralogisch Instituut te Utrecht.

Bij wijze van proef werd deze „sociologendag", die door 44 leden en introducé's werd bijgewoond, op een Zaterdag in plaats van een Zondag gehouden. Omdat de collegezaal van het Botanisch Laboratorium te Utrecht op Zaterdagochtend niet vrij was, werd een onderdak gevonden in het Geologisch-Mineralogisch Instituut. Om half elf opende de voorzitter, Dr A. SCHEYGROND, de vergadering en gaf het woord aan de eerste spreker, de heer H. T. WATERBOLK, die sprak over:

De natuurlijke bosvegetaties in Drente.

Het oorspronkelijke keileemplateau is doorsneden door beekdalen en op vele plaatsen bedekt met zanden. De huidige dorpen zijn ontstaan aan de rand der beekdalen. Daar vond men weidegrond, terwijl aan de andere zijde van het dorp de bouwlanden lagen, verenigd tot de es, meest door rooiing van bos verkregen. Nadat grote oppervlakten bos al sinds het *Neolithicum* waren vernietigd en vervangen door heide en akkerland zijn in historische tijd alle aanvankelijk zeker nog uitgestrekte wouden verdwenen op enkele kleine restjes na. Van vele dorpen wijzen de namen op vroeger bos, b.v. die op -lo: Anlo, Taarlo; op -elte (= holte): Uffelte, Wittelte en op -ter: Gasteren, Anderen. Veel bos is in de 80-jarige oorlog vernield. In de aanvang van de 17e eeuw werden door het landschapsbestuur plakkaten uitgevaardigd om het dreigende tekort aan eikenhout tegen te gaan. In de voorschriften van de laatste wolvenjacht (1772) leest men van allerlei bossen die thans verdwenen zijn. Op een stafkaart van 1840 komen nog een aantal natuurlijke bossen voor van meer dan 100 ha. Vanaf de vorige eeuw werden, vaak op of aan de rand der essen „ekkel- en telgenkampen" aangelegd. Zowel de oude resten — meest langs de rand der es gelegen en intact gelaten om de schaapskudden van de es te weren — als de jonge aanplant werden sindsdien als hakhout geëxploiteerd. Gelderse eekschillers verschenen in Drente. Beide bostypen zijn echter meestal duidelijk te onderscheiden op grond van ligging en vorm der percelen, effenheid van de bodem, bodemprofiel en vegetatie (homogeniteit, samenstelling, zeldzame soorten).

In de bosresten aan de rand der essen, vaak „strubben" genaamd, treft men meestal een duidelijke zonering aan, als gevolg van het feit dat het terrein iets helt en de keileem, die onder de es zeer ondiep ligt, aan de rand wegduikt met een nog steilere helling. Als deze zonering volledig is vindt men vanaf de esrand achtereenvolgens het *Querceto-Carpinetum*, het *Querceto-Betuletum violetosum*, het *Querceto-Betuletum typicum* en het *Querceto-Betuletum molinietosum*. Goede voorbeelden treft men langs de essen van Langelo, Zeijen, Eext, Schier, Anlo.

Kenmerkend voor het *Querceto-Betuletum violetosum* zijn naast *Pteridium*, *Majanthemum*, *Trientalis* en *Holcus mollis*: *Luzula pilosa*, *Convallaria*, *Hypericum pulchrum*, *Lathyrus montanus*, *Viola riviniana*, *Anemone nemorosa*, *Ajuga reptans* en *Anthoxanthum odoratum*. Als lokale (?) differentiërende soorten komen daarbij nog *Stellaria holostea*, *Polygonatum multiflorum* en *Hedera helix*. Merkwaardig is *Lathyrus montanus*, die van verschillende plaatsen bekend is, doch vooral veel voorkomt op de Bisschopsberg bij Havelte. Daar is de plant zelfs algemeen, met andere bosrelicten zoals *Anemone*, *Vaccinium* en *Majanthemum*, in het *Calluneta-Genistetum orchidetosum*, het heidegezelschap, dat de plaats van het bos heeft ingenomen, hier waarschijnlijk in de loop van de 18e eeuw.

Als differentiërende soorten van het *Querceto-roboris-Betuletum typicum* kunnen in Drente alleen gelden *Vaccinium vitis-idaea* en *Deschampsia flexuosa*. *Galium saxatile* en *Corydalis claviculata* komen in Drente in alle subassociaties van het *Querceto-Betuletum* voor, de laatste — evenals *Lonicera* — zelfs geregeld in het *Querceto-Carpinetum. Vaccinium myrtillus* en *Ilex* zijn in Drente typisch voor het *Querceto-Betuletum.* De genoemde planten blijken lokaal niet dezelfde sociologische waarde te bezitten als regionaal.

Alleen *Molinia coerulea* is typisch voor het vochtig zomereikenberkenbos. Vermeldenswaard is verder nog *Cornus suecica* in de Zeijerstrubben, die daar in het bos alleen voorkomt in de door het genoemde gezelschap ingenomen zone — en derhalve lokaal als differentiërende soort beschouwd moet worden — maar zijn optimale groeiplaats juist aan de noordrand van het bos vindt, waar dit grenst aan een *Ericetum.*

Terwijl de genoemde gezelschappen in Drente gelukkig niet zo zeldzaam zijn — al is de oppervlakte van de terreinen vaak zeer klein — zijn de *Querceto-Carpineta* veel minder algemeen. Op slechts enkele plaatsen wordt het *Querceto-Carpinetum typicum* gevonden (Eext, Langelo, Havelte), nl. daar waar in een strubbengebied de keileem zeer ondiep ligt. Het meest typisch voor dit gezelschap is wel de weelderige en soortenrijke struiklaag: *Corylus, Prunus avium, P. spinosa, Crataegus monogyna, C. oxyacantha, Evonymus, Malus silvestris, Ulmus suberosa, Fraxinus, Rosa canina* naast *Quercus, Sorbus, Betula* en *Populus tremula.* Ook *Fagus* komt plaatselijk voor. Door een pollenanalystisch onderzoek bij een opgraving van VAN GIFFEN kon bewezen worden, dat *Fagus* in de vroege bronstijd reeds lokaal (te Gasteren) voorkwam, doch elders (te Zeijen) tot ver in historische tijd heeft ontbroken. *Carpinus* werd nog niet in het wild aangetroffen, doch hoge percentages in een enkel pollendiagram wettigen het vermoeden, dat deze wel tot de natuurlijke Drentse flora hoort.

Zoals overal elders waren ook in Drente de *Querceto-Carpineta stachyetosum* en *filipenduletosum* oudtijds de rijkste bosgezelschappen. Er zijn echter nog slechts fragmenten over, meest in beekdalen met een keileemzool (Gasteren, Lieveren, Orvelte). Door ons werden hierin aangetroffen o.a. *Lysimachia nemorum, Carex pallescens, Rhamnus cathartica, Adoxa, Crepis paludosa, Listera ovata, Asperula odorata, Luzula maxima, Phyteuma nigrum, Gagea spathacea, Sanicula, Carex silvatica.* In de literatuur vindt men bovendien nog vermeld *Polygonatum verticillatum, Ranunculus auricomus, Paris* en *Equisetum silvaticum*! Zuivere associaten vindt men echter niet meer, ze zijn ten offer gevallen aan de ontginningen.

Ditzelfde geldt voor het befaamde *Alnetum cardaminetosum.* Er zijn nog enkele fragmenten met o.a. *Ribes nigrum, Impatiens noli tangere, Ajuga reptans, Cardamine amara, Chrysosplenium alternifolium, Festuca gigantea, Anemone nemorosa.* Wij vinden ze langs enkele beekjes in Noord-Drente. Meestal is daar echter alle bosopslag verdwenen en men mag dan blij wezen wanneer er nog geen verkaveling of herontginning heeft plaats gehad en enige der genoemde planten nog tussen het gras in de weiden te vinden zijn.

Meer naar de benedenloop van de riviertjes. d.w.z. in de randgebieden van de provincie is het *Alnetum typicum* oudtijds algemeen geweest. Goede voorbeelden van dit gezelschap moet men echter buiten Drente zoeken, b.v. in de eendenkooien van N.-W. Overijsel.

De tweede voordracht: *Regulerende elementen in de dierlijke samenleving*, werd gehouden door Dr A. D. Voûte; hiervan werd geen samenvatting ontvangen. De derde spreker was de heer Th. A. de Boer, die tot onderwerp had:

Plantensociologische waarnemingen op geïnundeerd grasland.

Bij grasland hebben we met een grote verscheidenheid van plantengezelschappen te maken. Door allerlei invloeden, hoofdzakelijk van de mens, maar ook van het weer, kunnen er meer of minder sterke veranderingen in deze gezelschappen plaats vinden. Al naar gelang van de sterkte dezer invloeden, kunnen er veranderingen in de soortencombinatie, frequentie of massaverhouding der soorten plaats vinden.

Nu is de invloed van een inundatie, ten minste als deze gedurende een gedeelte of het gehele groeiseizoen plaats vindt, zo ingrijpend, dat de aanblik van het grasland de eerste jaren geheel is gewijzigd.

In 1944—'45 is ± 10% van het Nederlandse grasland geïnundeerd geweest, waarvan het meeste met een totaal verrotte zode boven kwam. Hierop ontwikkelden zich, al naar gelang van de ligging van het perceel t.o.v. de grondwaterspiegel, grondsoort, vruchtbaarheidstoestand van de bodem en gebruik van het grasland voor de inundatie, verschillende plantengezelschappen. Natuurlijk had de behandeling na het droogkomen invloed op de begroeiing, maar ingeval deze niet van ingrijpende aard was, dan bepaalden toch in hoofdzaak de hierboven genoemde factoren het karakter en de successie van de herbegroeiing.

Door middel van een 120-tal observatievelden van een $^1/_2$ are oppervlakte, die geregeld op plantensoorten, hun massaverhouding en de zodedichtheid werden waargenomen, konden we tot een indeling naar plantengezelschappen komen, die verband hielden met de oecologische factoren.

Opvallend is de dominantie van één enkele plantensoort of althans van een gering aantal plantensoorten, een verschijnsel dat we altijd bij extreme milieu-omstandigheden vinden.

De successie van deze vegetaties verloopt zeer langzaam, vooral op de meer laagliggende observatievelden. Over het algemeen is de homogeniteit nog zeer gering. Het aantal soorten neemt slechts langzaam toe. Bij sommige typen, waar in de aanvang veel tweezaadlobbigen stonden, is het aantal soorten zelfs gedaald.

Waarschijnlijk hebben veel graszaden de inundatie overleefd, maar waren voor allen de kiemomstandigheden niet gunstig. De prioriteit, die sommige soorten hierdoor verkregen, heeft de mogelijkheid van uitbreiding van andere soorten zeer belemmerd. In echte weiden, waar veel grassoorten geen zaad kunnen vormen, traden deze soorten na de inundatie ook niet op. Duidelijk is dit het geval voor *Lolium perenne*, die op de hooilanden, van goede kwaliteit, wel verscheen, doch op de echte weilanden niet.

Tot slot laten we nog de plantengezelschappen, die naar de dominerende soorten zijn genoemd, volgen:

a. bij zoetwater-inundatie de gezelschappen van: 1. *Glyceria*, 2. *Agrostis stolonifera*, 3. *Alopecurus geniculatus*, 4. *Poa annua* en *Plantago major* en 5. *Triticum repens*.

b. bij zoutwater-inundatie de gezelschappen van: 6. *Atriplex* en 7. *Spergularia* en *Salicornia*.

Op de oecologie ervan kunnen wij hier niet nader ingaan; wij verwijzen naar het uitvoerige artikel, dat in dit tijdschrift binnenkort zal verschijnen.

Hierna sprak Ir P. TIDEMAN over:

Flora van de garrigues in de Franse Midi. Oecologische en genetische opmerkingen over enkele van zijn plantengezelschappen in verband met de mogelijkheden tot beter bodemgebruik.

Het glooiende heuvelland rondom Montpellier, tussen Cevennen en zeekust gelegen, is opgebouwd uit kalkgesteenten van Jura-krijt en tertiaire formaties. Dit bijkans noordelijkste punt der Mediterrane regio kent een extreem droge en hete zomer naast een vochtig, koel voorjaar, een aan slagregens rijk najaar en een milde winter.

Met de uitgestrekte wijngaarden zijn het vooral de garrigues, die het aspect van het landschap bepalen. Deze halfnatuurlijke, struikachtige begroeiing is na velling, herhaald afbranden en door vraat van talrijke zwervende schaapskudden uit het natuurlijke altijdgroene-eikenbos (*Quercetum ilicis*) ontstaan. Door de geweldige oppervlakte, die deze extensieve cultuur inneemt en door de sterke mate waarin deze aan de eroderende werking der stortregens onderhevig is, vormen de garrigues het grootste gevaar voor de welvaart van deze streek.

Uitgaande van het *Quercetum ilicis*, de floristisch opvallend gelijkvormige op de meest uiteenlopende moedergesteenten voorkomende climax-associatie, vertoont de regressieve successie onder invloed van bovengenoemde opeenvolging van anthropogene factoren een sterke differentiatie van de vegetatie op de verschillende uitgangsgesteenten. Dit is enerzijds het gevolg van de door afspoeling geleidelijke afbraak van het A.B.C.-profiel der climax-associatie (dikwijls tot op het kalkgesteente), anderzijds wordt dit veroorzaakt door de toenemende gevoeligheid der begroeiing voor het edaphisch milieu.

Twee bodemtypen zijn van belang: In de eerste plaats dat der gele gronden op het krijt, eoceen, mioceen en plioceen. Slecht doorluchte, moeilijk vochtdoorlatende plastische structuurloze lemen met een hoog kalkgehalte en dientengevolge veelvuldig voorkomende reversibele uitvlokkingen en irreversibele concreties van $CaCo_3$. Plaatselijke gley-verschijnselen. Daarnaast het bodemtype der rode gronden op de compacte jura-kalk-gesteenten. Goed geaëreerde, gekruimelde grond met relatief laag kalkgehalte.

Reeds het eerste degradatie-stadium: het *Quercetum cocciferae*, valt in twee naar bovengenoemde bodemtypen scherp gescheiden subassociaties uiteen. Voortgaande devastatie voert op de gele gronden in hoofdzaak via het *Rosmarineto-Lithospermetum*, op de rode gronden via het *Brachypodietum ramosi* naar volledige ontbloting van het moedergesteente. Beide laatstgenoemde gezelschappen vertonen een duidelijke aanpassing aan de extremen van klimaat (zomerdroogte) en milieu. Het biologisch spectrum van het *Rosmarineto-Lithospermetum* geeft het hoogste aantal *chamaephyta* (altijd groene halfstruiken, 50%), dat van het *Brachypodietum ramosi* het hoogste gehalte aan therophyten (42%) van alle noordmediterrane gezelschappen. Voor beide geschiedt de zaadverspreiding voornamelijk in de zomer. Jaarcurven van transpiratie en osmotische druk van verschillende kensoorten van het *Rosmarineto-Lithospermetum* tonen aan, dat door de xeromorphe bouw der planten het evenwicht in de waterhuishouding ook in de critieke jaargetijden (zomer en in mindere mate de winter) gewaarborgd is.

In dit gezelschap nu blijkt *Pinus halepensis*, zelfs op de sterk door erosie aangetaste terreinen, van nature op te slaan en indien deze zeer brandgevaarlijke soort voor zomerbranden gespaard blijft, vertoont zij een goede groei. Eerst onder het scherm van *Pinus halepensis* vinden vele soorten uit het *Quercetum ilicis* het voor hun ontkieming benodigde microklimaat. Zo kan zich langs natuurlijke weg op de gele gronden het *Quercetum ilicis* via het *Rosmarineto-Lithospermetum pinetosum* sneller herstellen dan via het *Quercetum cocciferae* mogelijk is. Op de rode gronden daarentegen blijft natuurlijke opslag van *Pinus halepensis* achterwege en kan deze zich, indien kunstmatig aangeplant, slechts als een kreupele, oppervlakkig wortelende en sterk door parasieten aangetaste boom ontwikkelen. Hier voert de natuurlijke regeneratie, bij uitsluiting van brand, kap en vraat, via het *Quercetum cocciferae* naar het *Quercetum ilicis* terug. terug.

Voortgaande op het reeds door de Romeinen ingestelde en sindsdien ontaarde *silva-saltus-ager* stelsel (bos, veeweide-plaats en akker) kan men zich de bestrijding van het erosiegevaar en de intensivering van het bodemgebruik voorstellen door o.a.:

de *silva* uit te breiden door bosaanleg vooral op de voor erosie gevoelige kalkmergel-gronden, op waterscheidingen en langs waterlopen, waar mogelijk met behulp van *Pinus halepensis* als pionier;

de *saltus* tegen bos en akkers duidelijk af te perken, de beweidingsmethoden te verbeteren (uitsluiting van brand), de opbrengst met inzaaien van grassen en leguminosen op de rode gronden te verhogen en het schaap waar mogelijk door minder talrijk hoornvee te vervangen.

Tot de uitvoering van dit urgente welvaartswerk kan de plantensociologie als toegepaste wetenschap met vegetatie-onderzoek en -kartering een onmisbare bijdrage leveren.

De laatste spreker was de heer H. J. ZWART, die tot onderwerp had:

De vegetatie van de brongebieden in de Lutte.

Alvorens de vegetatie van de brongebieden te behandelen, volgt eerst een kort overzicht van de ontstaanswijzen en het voorkomen van deze brongebieden. Het blijkt dat deze te vinden zijn in diep ingesneden beekdalen, die we in de hooggelegen stuwwal van de Lutte en ook van Ootmarsum kunnen vinden. In deze beekdalen komt het, over ondoorlaatbare kleilagen dóór daarop liggend zand, stromende water — regenwater — terecht, en verschijnt hier aan de oppervlakte door het uitwiggen van de zandlaag.

Onder de planten, die in deze beekdalen voorkomen, zijn er een aantal, die een duidelijke voorkeur voor deze standplaats hebben, b.v. *Chrysoplenium oppositifolium*, *Cardamine amara*, *Montia*, *Stellaria alsine*, *Brachythecium rivulare*.

De successiereeks in deze brongebieden is als volgt: *Philonotis fontana - Montia rivularis* - associatie → weidegezelschap verwant aan *Cirsium oleraceum - Angelica silvestris* associatie → *Alnetum glutinosae cardaminetosum* - *Querceto-Carpinetum filipenduletosum*, variant met *Cardamine amara*.

De pionierassociatie van *Philonotis fontana* en *Montia rivularis*, heeft behalve deze twee genoemde soorten *Montia lamprosperma* en *Stellaria alsine* tot associatiekensoorten; verbondskensoorten zijn *Brachythecium rivulare* en *Chrysosplenium oppositifolium*. De associatie is onder te verdelen in drie subassociaties, nl. een typische op „Quellfluren", een subassociatie met differentiërende soorten *Isolepis setacea, Juncus bufonius* en *Sagina procumbens,* — een overgang naar het *Isolepeto-Stellarietum* — te vinden in gegraven greppeltjes in beekdalen, en tenslotte een subassociatie in beekjes met *Callitriche verna* en *Potamogeton oblongus*.

Het volgende successiestadium is meestal één of ander weidegezelschap óf soms direct het bronnetjesbos. Van die weidegezelschappen is weinig te zeggen. Een aantal is verwant met de in Westfalen voorkomende *Cirsium oleraceum-Angelica silvestris* associatie. Verder vinden we associaties van het *Filipenduletum: Juncetum acutiflori, Caricetum canescentis fuscae* en *Juncetum filiformis*.

De climaxassociatie op brongebieden is moeilijk te bestuderen, tengevolge van de schaarste van geschikte terreinen voor dit gezelschap. Uit fragmenten, die we op verschillende plaatsen vonden, leek het ons waarschijnlijk, dat het eerst optredende bos een *Alnetum* is, met als extra-soorten naast die van het *Alnetum typicum: Chrysosplenium oppositifolium, Cardamine amara, Chrysosplenium alternifolium* en *Brachythecium rivulare*. Kensoorten uit het *Querceto-Carpinetum* komen niet of practisch niet in dit bos voor. De grondwaterstand is zeer hoog, nl. gelijk aan het maaiveld. Dit gezelschap is het *Alnetum glutinosae cardaminetosum amarae* Meyer Drees 1936. Door de grote hoeveelheid plantenresten-producten zal er een vervening optreden, met als gevolg een droger worden van de oppervlakte. Planten uit het *Querceto-Carpinetum* doen hun intrede, b.v. *Ranunculus Ficaria, Adoxa moschatellina, Anemone nemorosa, Lamium Galeobdolon, Ajuga reptans, Fraxinus excelsior*. Het bos begint veel op een *Querceto-Carpinetum filipenduletosum* te lijken, alleen blijven *Chrysosplenium oppositifolium* en *alternifolium, Cardamine amara* en *Brachythecium rivulare* voorkomen, om welke reden we dit bostype als een variant van *Cardamine amara*, met bovengenoemde planten als differentiërende soorten zouden kunnen beschrijven.

In het buitenland zijn een aantal bosgezelschappen beschreven, die nauw met zojuist genoemd bostype verwant zijn, maar meest op meer kalkrijke bodem groeien.

VERSLAG van de Twintigste Nederlandse Dag voor Biosociologie en Palaeobotanie, gehouden op 23 November 1947 in de collegezaal van het Botanisch Laboratorium te Utrecht.

Blijkens de presentielijst werd deze dag bijgewoond door 39 leden en 6 introducé's, Nadat om half elf de voorzitter, Dr A. SCHEYGROND, de vergadering geopend had, gaf hij het woord aan de eerste spreker, de heer J. J. BARKMAN, die sprak over:

Enige epiphytenassociaties in Zwitserland.

Tijdens deze voordracht deed spreker mededeling van de resultaten van een phytosociologisch onderzoek, door hem tijdens een verblijf in Zwitserland in 1946 verricht. Enkele der Zwitserse epiphytenassociaties, door OCHSNER in zijn dissertatie (1928) zo voortreffelijk behandeld, konden door hem niet bestudeerd worden. Drie hiervan had spreker gelegenheid nader te onderzoeken, te weten het subalpine *Letharietum vulpinae*, het subalpine *Cetrarietum pinastri* en het mediterrane *Fabronietum pusillae.* Wegens tijdgebrek konden hier slechts de resultaten betreffende het *Lethariestum* vluchtig gereleveerd worden. Vooraf ging een overzicht over de belangrijkste epiphytenassociaties der Alpen en hun verdeling over de verschillende vegetatiegordels. Sommige epiphytenassociaties zijn strikt aan één vegetatiegordel gebonden (bijv. het *Lethariestum vulpinae* en het *Usneetum barbatae*), andere zijn plurizonaal (bijv. het *Physcietum ascendentis*).

Het *Lethariestum vulpinae* is gebonden aan de *Larix-Pinus Cembra*-gordel sensu SCHMID = *Rhodoreto-Vaccinietum*-climaxcomplex Br.-Bl.p.p. en komt dus, evenals deze gordel, in de Alpen slechts tussen 1700 en 2400 m. zeehoogte voor. De dikwijls lager (in het *Piceetum*-climaxcomplex) aangeplante Larixen dragen geen *Lethariestum*, maar het bij deze gordel behorende *Usneetum barbatae.*

Het *Lethariestum* is gebonden aan *Larix* en *Pinus Cembra* als substraat, ontbreekt dus evenals deze boomsoorten in de N.- en Z.-Vooralpen, en is tot de Centrale Alpen (Wallis, Gotthardmassief, Engadin) beperkt. In alle drie gebieden werden opnamen gemaakt.

Het is een 2-lagige associatie van struik- en bladvormige lichenen. Aspectbepalend zijn de felgele pruiken van de dominante kensoort *Letharia vulpina.* Een onopvallende, maar trouwe kensoort is de zeldzame *Parmelia austerodes.* Hoogpresente (4 en 5) begeleiders zijn *Parmelia furfuracea*, *Alectoria iubata* en *Parmeliopsis ambigua.*

De associatie behoort tot het *Usneion*; evenals het hele verbond is zij photophiel, toxi- en nitrophoob en acidiphiel. In de toch al lichte *Larix*-parkbossen bekleedt zij slechts bomen aan de bosrand of aan open plekken; vaak groeit zij op de uiterste einden van dode, naakte takken. Vaak op steile W.-N.-hellingen, en meestal op de W.-N.O.-zijde van de stammen. De associatie komt voor op de schors van *Larix*, maar alleen op het dode hout van *Pinus Cembra*, en mijdt diens schors absoluut (giftige stoffen?). Bij een helling van 80°-90° domineert *Letharia vulpina*, bij een helling van 60°-80° *Alectoria iubata*, bij 0°-50° (takken) *Parmelia furfuracea.*

Het *Lctharietum* is een climaxassociatie. Over de voorafgaande successiestadia (korstvormige lichenen) is nog niets bekend. De associatie sluit zich meestal niet geheel: door afbladeren van de *Larix*-schors, bosbranden en afrukken van *Letharia*-pruiken door de wind vallen telkens plekken open, die echter spoedig weer door talrijke kiemplantjes van *Letharia vulpina* worden opgevuld.

In het *Piceetum* en in de *Larix-Pinus Cembra*-gordel zijn de boombases met het *Cetrarietum pinastri* begroeid. In het *Piceetum* bekleedt het *Usneetum* stam en takken; in de *Larix-Pinus Cembra*-gordel „schuift” zich tussen beide associaties het *Letharietum* in, en „verdrijft” het *Usneetum* met toenemende zeehoogte steeds hoger de kroon in. Tenslotte valt het *Usneetum* geheel uit.

Over de geografische verspreiding van het *Letharietum* is nog niets bekend, maar, gezien de verspreiding van *Letharia vulpina*, waarschijnlijk het subarctisch-subalpine gebied van het hele N. halfrond beslaand. In N. Amerika fructificeert *Letharia vulpina*, in Europa niet. Tenslotte werd herbariummateriaal van een aantal der besproken lichenen gedemonstreerd.

De tweede spreekster was Mej. A. C. STOLK, die als onderwerp had:

Het Pollenanalytisch Onderzoek van het Haaksbergerveen.

Het Haaksberger veen ligt in het Z.O. van de provincie Overijsel ten Z. van Haaksbergen. Het veen ligt op een pleistocene ondergrond van laagterras en keileem. Op verschillende punten van dit veengebied werden boringen gedaan. Hier zal slechts een van deze boringen worden besproken. Het pollendiagram begint met een tamelijk warm spectrum. *Pinus* is dominant, verder zijn aanwezig *Betula*, *Corylus*, *Alnus*, *Quercus* en *Salix*. *Corylus* en *Alnus* bereiken ongeveer ieder 10%.

Deze warme periode gaat vooraf aan een koude tijd. Ook de andere diagrammen van het Haaksberger veen beginnen met spectra uit een warmere tijd, waarop dan een koude periode volgt. Hetzelfde verschijnsel wordt ook in vele andere Nederlandse diagrammen gevonden b.v. in de diagrammen van Wijster, Grollo, Hurenerveld, Deurnse Peel II en Zeyen. Deze warmere spectra worden algemeen toegeschreven aan een interstadium of Interglaciaal.

Volgens Waterbolk gaat het hier om afzettingen uit het laatste deel van het Interstadiaal tussen Würm I en Würm II, dat is het Twentse Interstadium.

Op deze interstadium-afzettingen volgen afzettingen uit de toendratijd. Hier treedt een zeer hoog % *Cyperaceeën* op, nl. 2600%, *Salix* bereikt een maximum van 41%, verder zijn micro- en macrosporen van *Selaginella selaginoides* aanwezig, de microsporen tot 30,7%.

Op deze toendra-spectra volgen subarctische spectra met grote % *Pinus* en *Betula* en een klein % *Salix*, terwijl het thermophiele element geheel ontbreekt.

Preboreale afzettingen ontbreken in dit profiel.

De boreale *Pinus* en *Corylus*-toppen zijn in dit diagram zeer duidelijk. Nadat *Pinus* en *Corylus* hun boreale maxima hebben bereikt, dalen beide. De stijgende *Alnus*-curve snijdt de *Pinus*-lijn. Hier begint het Atlanticum. Het verdere verloop van dit diagram in Atlanticum, Subboreaal en Subatlanticum komt geheel overeen met andere diagrammen uit het O. van ons land, vooral de overeenkomst met de diagrammen van het Korenburgerveen en het Aamsveen is zeer groot. In deze diagrammen treedt *Fagus*, evenals in het Haaksbergerveen al vroeg in het Atlanticum op, en boven de grenshorizon bereikt *Fagus* een hoog maximum. Dit bedraagt in het Haaksbergerveen 41%. De meer N. gelegen venen bij Vriezenveen, Hurenerveld, Grollo en Wijster onderscheiden zich van het Haaksbergerveen door veel lagere *Fagus*-waarden. Bovendien begint de *Fagus*-curve in deze N. venen later dan in het Haaksbergerveen.

Dit verschil in voorkomen van de beuk vinden we echter ook in de tegenwoordige tijd. Het Haaksbergerveen valt, evenals het Korenburgerveen en het Aamsveen, in het subcentreurope district van van Soest, waarin de beuk een grote rol speelt, terwijl Vriezenveen, Hurenerveld, Grollo en Wijster er buiten vallen. Hieruit blijkt dus, dat daar waar thans oecologisch de beste groeimogelijkheden voor de beuk zijn, het stuifmeel van deze boom het eerste en in het hoogste % optreedt.

In het Buurserveen, dat in het O. aan het Haaksbergerveen grenst, is een stenen bijltje gevonden. Dit is volgens Hijszeler afkomstig uit het Laat-Neolithicum ± 2000 v. Chr. Het aanklevende veen is pollenanalytisch onderzocht. Pollenanalytisch bleek dit bijltje te vallen in het Atlanticum (*Fagus* 0.7% *Corylus* 33.3%, *Pinus* 23%, *Alnus* 37%). Het spectrum van dit bijltje kan gevoegd worden in het diagram van het Haaksbergerveen, waardoor dit deel van het diagram kon worden gedateerd op 2000 v. Chr.

In het Haaksbergerveen bleek een veenbrug aanwezig te zijn.

Van dit profiel met veenbrug werd een serie monsters verzameld en deze werden pollenanalytisch onderzocht. Deze brug, die een verbinding moet hebben gevormd tussen Almelo en Haaksbergen, lag 15 cm. onder de grenshorizon. De brug bestond uit berkenstammen en takken. Het spectrum bij de veenbrug o.a. bevatte 7% *Fagus*, *Carpinus* was juist aanwezig (0.7%), *Corylus* was slechts 9%. De veenbrug stamt dus uit het Subboreaal.

De derde voordracht, gehouden door de heer D. BAKKER, was getiteld:

De flora en fauna van Walcheren tijdens en na de inundatie.

In October 1944 bombardeerden de geallieerden de dijken van Walcheren. Op vier plaatsen stroomde het zoute buitendijkse water het eiland binnen. Het grootste gedeelte van Walcheren werd dagelijks aan de eb- en vloedstromen blootgesteld. Het gebied westelijk van het kanaal door Walcheren, groot 13500 ha, kwam na een overstroming van één jaar weer droog. In de Zuidwatering, oostelijk van het kanaal gelegen en 2200 ha groot, had de zee tot Februari 1946 vrij toegang.

Met de getijstromen kwamen vele organismen, meestal in het larvenstadium, het eiland binnen. Vooral mossels, kokkels en zeepokken breidden zich sterk uit. De planten en dieren groeiden in korte tijd tot forse, krachtige individuen uit, hetgeen op een gunstig milieu wees. Toch was deze binnenzee nog betrekkelijk soortenarm. De korte overstromingsperiode kan hier ongetwijfeld aansprakelijk voor gesteld worden.

Van de planten overleefde *Tamarix gallica L.* de inundatie in zijn geheel. Van riet, zeebies en kweek bleven slechts enige onderaardse delen in leven. Van *Veronica hederifolia L.* kiemden de zaden nog na de inundatie in een zoet milieu. In de zoute bosgrond van Walcheren trad van deze soort geen ontkieming op. Van verschillende soorten kiemden de zaden massaal. Deze soorten kregen zelfs een veel grotere verbreiding dan voor de inundatie (*Atriplex hastata L.*, *Chenopodium serotinum L.*).

Het bodemmilieu was door de overstroming sterk gewijzigd. De bodem werd overal, gemiddeld tot een diepte van 1 m, bremzout. Onder de anaerobe omstandigheden trad sulfaatreductie op. Het natrium uit het keukenzout deed natriumklei ontstaan. Op vele plaatsen werden zand- en sliblagen afgezet. Ook was de grond de eerste tijd zeer rijk aan stikstof in een voor de plant opneembare vorm.

Het ontziltingsproces ging op de lichte zavelruggen vrij snel (oude stroomgeulen). Op de zware komgronden ontziltte de bodem veel minder vlug.

Het eerste jaar ontplooide zich een begroeiing van éénjarige, stikstofminnende voorjaarskiemers met een hoge zouttolerantie (*Atriplex hastata L.*, *Chenopodium spec.*). Op de snel ontziltende, goed geaëreerde zavelruggen kwamen hetzelfde jaar ook reeds verschillende grassen en klaversoorten voor (*Agrostis stolonifera L.*, *Medicago arabica Huds.*). Op de zware komgronden, waar onder invloed van de regenval en verdamping grote schommelingen in zoutgehalte voorkwamen en de bodem tevens slecht geaëreerd was, domineerden *Puccinellia distans Parl.* en *Spergularia salina Presl.*

De fauna was zeer arm aan soorten. Enkele plagen traden op (*Plusia gamma L.*).

Vervolgens sprak Ir P. DEN DULK over *De vegetatie van de voormalige blauwgraslanden van het Binnenveld bij Wageningen.* Van deze voordracht werd geen samenvatting ontvangen. De laatste spreker was Dr V. WESTHOFF met een mededeling, getiteld:

De plantengroei van de Botshol (bij Abcoude).

De Botshol vormt een schakel in de keten van water- en moerasgebieden met afnemend zoutgehalte van het brakke Waterland tot het zoete Kortenhoef en Loosdrecht. Tengevolge van het inlaten van brak water uit de Waver in de zomermaanden (waardoor het sterk naar de droogmakerij Groot-Mijdrecht wegkwellende water van Botshol op peil gehouden moet worden) schommelt het chloorgehalte vrij sterk: in 1942 en 1943 tussen 570 en 1325 mg per l met een gemiddelde van 900 mg. Botshol ligt dus op de grens van de oligohaliene en de mesohaliene zone. Voorts is het water carbonaatrijk, de ondergrond bestaat uit met slib bedekte zandige klei, de pH van het open water varieert van 7,0-7,4 en de invloeden van de mens zijn zeer sterk en gevarieerd. Nagegaan is, hoe al deze en andere factoren zich nauwkeurig weerspiegelen in de samenstelling van flora en vegetatie. In het gebied zijn 283 soorten phanerogamen, 62 soorten bryophyten, 35 soorten fungi en 23 soorten macroscopische algen waargenomen. Voorzover de phanerogamen en mossen betreft is de inventarisatie nagenoeg compleet te noemen. 45 der phanerogame spp. zijn ruderaal en adventief, 70 stenassociatief (stenoek), 15 min of meer zeldzaam (o.a. *Carex hostiana*, *C. pulicaris*, *Cirsium dissectum*, *Cladium mariscus*, *Epipactis palustris*, *Fritillaria meleagris*, *Liparis loeselii*, *Naias marina*, *Ophioglossum vulgatum*, *Orchis incarnata*). Bij vergelijking met het mesohaliene gebied van Noordholland blijken 10 halophyten in Botshol te ontbreken (beperkende factor: Cl-‰ in winter; vb. *Althaea*), terwijl 5 aldaar ontbrekende glycophyten ± talrijk in Botshol voorkomen (vb. *Nymphaea*) en 13 andere er sporadisch zijn (vb. *Butomus*). Voor deze laatste valt de grens van het tolerantiegebied blijkbaar samen met de grens oligohalien-mesohalien. Bij vergelijking met het zoete gebied van b.v. Kortenhoef blijken in Botshol nog 5 facultatieve halophyten op te treden (vb. *Samolus*) die ginds niet meer of niet meer vegetatievormend voorkomen, terwijl van een aantal in Botshol voorkomende soorten aannemelijk kan worden gemaakt, dat zij hier het relatief hoge Cl-‰ en in het bijzonder de schommeling daarin vermijden (vb. *Hottonia*).

Botshol wordt gevormd door 105 ha water, 31 ha rietland, 61 ha mager rietland (*Sphagnum*-rijk rietland, *Valerianeto-Filipenduletum*, blauwgrasland), 142 ha bemest grasland, 6 ha bouwland en een wisselend, doch klein percentage van telkens gekapte of gerooide en elders weer opschietende bosjes. De vegetatie werd bestudeerd met uitsluiting van bouwland en bemest grasland. Aangezien goed ontwikkelde associaties slechts een kleine minderheid van het gebied vormen (de oorzaken hiervan werden uiteengezet) en vele gezelschappen er beter gekenmerkt zijn door dominantie in hun verschillende étages, werden voor de onderscheiding der vegetatieeenheden de Scandinavische (sociatie, consociatie) en de Frans-Zwitserse (associatie) methode naast elkaar gebruikt, zodat zij elkaar aanvulden, echter onder toepassing van een uniforme Fr.-Zw. analytische techniek. De successie-stadia zijn zo goed mogelijk vastgesteld (een schema daarvan werd gedemonstreerd) en als bouwstenen voor de te onderscheiden eenheden gebruikt.

In het open water der plassen treft men vooral een *Chara hispida*-sociatie aan (pH 7,0-7,3), wier concurrerend vermogen en systematische plaats (*Charetalia*? *Potametalia*?) besproken werden; voorts het meso- en oligohalinophiele gezelschap van *Naias marina* en *Nitellopsis obtusa*, verwant aan het *Parvopotameto-Zannichellietum* W. Koch. Tot de sloten beperkt is het *Hydrochareto-Stratiotetum*, hier goed ontwikkeld, hoewel aan de grens van zijn zouttolerantie; het is gebonden aan een lage pH en gaat op O_2-rijkere plaatsen over in een facies van *Utricularia vulgaris* en *Vaucheria* sp. Onder de oeverbegroeiingen (*Phragmitetalia*) valt het meest op de sociatie van *Cladium mariscus* (pH in de wortellaag 7,2-7,0, gebonden aan een eutroof milieu (stenobasiphiel), maar het mesohalinicum mijdend, aan haar chloorgrens (zoals in Botshol) blijkbaar een O_2-rijk milieu eisend en vermoedelijk derhalve hier gebonden aan oevers van plassen met krachtige golfslag. Vermelding verdient voorts het *Scirpetum maritimi*, dat in het meest brakke N. van

Botshol (max. 1275 mg Cl per l) nog voorkomt, doch in het Z.deel (max. 940 mg per l) zijn Cl-grens blijkbaar naar beneden overschrijdt en hier uiteenvalt in zijn componenten (*Scirpus maritimus* en *Schoenoplectus tabernaemontani*), daar verspreid groeiend in fragmentair *Scirpeto-Phragmitetum.* — Aangetoond werd voorts, dat de oecologische amplitudines van *Carex inflata* en *Carex vesicaria* elkaar nauwelijks raken en dat de associatie *Caricetum inflato-vesicariae* W. Koch 1926, berustend op onvoldoende materiaal, dient te vervallen. Men kan inplaats daarvan het ook in het Botshol vertegenwoordigde *Caricetum gracilis-vesicariae* opstellen.

De rietlanden van Botshol vormen in hoofdzaak een ingewikkeld complex van sociaties, waarin *Phragmites* steeds de hoge kruidlaag vormt, terwijl de moslaag doorgaans bestaat uit sociaties van *Sphagnum plumulosum*, *S. palustre* en soms *Aulacomnium palustre* (grondwater 0-6 cm onder het maaiveld), op droger terrein verdrongen door *Dicranum Bonjeanii* en tenslotte door *Polytrichum commune* (grondwater 10-25 cm onder maaiveld). De pH in de rhizosfeer van deze *Phragmites-Sphagnum* + *Dicranum*-consociatie varieert van 4,5 tot 5,2 (actieve verzuring door *Sphagnum*!) 11 opnamen van dit gezelschap bevatten 80 soorten phanerogamen, d.i. $\frac{1}{4}$ van de flora van Botshol; deze soortenrijkdom bestaat voor een groot deel uit verbonds- en ordekensoorten van het *Caricion canescentis-fuscae* en het *Molinion.* Opmerkelijk is, dat deze twee groepen steeds tezamen voorkomen en dat de initiale phase van de consociatie zich niet kenmerkt door een overwicht van *Caricion*-soorten, doch door halophyten en relicten uit de *Phragmitetalia.* De mogelijke oorzaken van dit verschijnsel, alsmede de synoecologie van het gezelschap (o.a. het „massa-effect" van de *Sphagnum*-populatie, die kan leven bij een Cl′-concentratie, welke de afzonderlijke *Sphagnum*-plant niet meer verdraagt), werden besproken. Als overige gezelschappen der *Molinietalia* komen nog voor het oligohalinophiele oevergezelschap van *Sonchus paluster*, de goed ontwikkelde associatie *Valerianeto-Filipenduletum*, welke hier 6 kensoorten telt (*Valeriana officinalis*, *Euphorbia palustris*, *Stachys palustris*, *Lathyrus paluster*, *Festuca arundinacea*, *Crepis paludosa*) (pH rhizosfeer 5,0-6,1) en tenslotte het *Cirsieto-Molinietum*, het blauwgrasland (pH rhizosfeer 4,6-5,8). Het *Cirsieto-Molinietum* begroeit de oude kernen van het gebied, de zgn. legakkers, d.i. het weinig of niet afgegraven veen. Afgeveende legakkers, alsmede de „aanwassen", d.z. de door verlanding ontstane terreinen, zijn bekleed met de *Phragmites-Sphagnum*-consociatie, terwijl de „andammen", d.z. de door de mens met slootbagger en vuil opgehoogde aanwassen, de groeiplaatsen vormen van het gezelschap van *Sonchus paluster* en het *Valerianeto-Filipenduletum*.

Tenslotte werden de bosjes van Botshol (*Alnetum* en *Betuleto-Salicetum*) kort besproken. 7 vegetatietabellen lichtten een en ander nader toe.

VERSLAG van de Commissie voor de bescherming van de Wilde Flora over 1947.

In de vacature, ontstaan door het periodiek aftreden van J. G. SLOFF, werd voorzien door verkiezing van Dr W. H. DIEMONT. Het secretariaat werd waargenomen door ondergetekende.

In enige gevallen, waar de inheemse flora gevaren dreigen, zijn door de Commissie stappen gedaan teneinde te trachten deze gevaren af te wenden.

Zo is aan de Vereniging tot Behoud van Natuurmonumenten in Nederland verzocht maatregelen te treffen tot drastische beperking van het aantal konijnen op Voorne, daar anders de waarschijnlijkheid groot is, dat zich de bijenorchis (*Ophrys apifera*) en andere zeldzame plantensoorten op dit eiland niet zullen kunnen handhaven.

Bij het Provinciaal Bestuur van Noord-Holland is aandacht gevraagd voor het behoud van de groeiplaats van de vogelnestorchis (*Neottia nidus-avis*) en de koraalwortel (*Corallorrhiza trifida*) in de duinen bij Bergen, welke groeiplaats gevaar loopt ingrijpend te worden gewijzigd bij de in dit duingebied voorgenomen aanleg van een waterwinplaats.

Voorts is adhesie betuigd aan een adres van de Commissie voor de Biosociologie en het Veenonderzoek aan de Ministers van Onderwijs, Kunsten en Wetenschappen en van Landbouw, Visserij en Voedselvoorziening in zake het behoud van het Beerse-dal benoorden Spoordonk.

Aan de Directie van het Staatsbosbeheer werden inlichtingen verstrekt over de verspreiding van *Scutellaria minor* in ons land.

Zowel door de Provincie Noord-Holland als door de Vereniging tot Behoud van Natuurmonumenten is toegezegd de flora zo goed mogelijk te zullen beschermen.

Wij zijn hiervoor dankbaar en hopen de bedreigde flora ook in de toekomst nog te kunnen waarnemen en bestuderen.

De Secretaris,
J. VLIEGER.

VERSLAG Commissie voor Phytopathologie over 1947.

Op de jaarvergadering in Februari 1947 werd Dr J. W. M. Roodenburg als lid van de Commissie voor Phytopathologie herkozen. De vergadering keurde een statutenwijziging goed, waarbij de Commissie toestemming kreeg, personen, die geen lid zijn van de Kon. Ned. Botanische Ver., toe te laten als „contribuanten"; tegen een bijdrage van *f* 2.— per jaar hebben deze contribuanten het recht, de vergaderingen, belegd door de Commissie voor de Phytopathologie, te bezoeken. Als contribuant hebben zich 11 personen aangemeld.

19 April 1947 werd een vergadering gehouden in het Laboratorium „W. Commelin Scholten" te Baarn, met de volgende sprekers:

Drs J. P. Bels over: Enkele ziekten en plagen van de champignoncultuur;

Mej. Dr J. C. Went over: Phytopathologische waarnemingen omtrent boomziekten op een reis naar Engeland;

Mej. A. L. van Beverwijk: Indrukken van Engelse laboratoria; bespreking van enige mycologische methoden.

Op 20 December 1947 werd te Wageningen vergaderd. Gesproken werd door:

Prof. K. C. Winkler: Resistentie en Immuniteit, gezien van medisch standpunt;

Prof. Dr H. M. Quanjer: Resistentie en Immuniteit, gezien van botanisch standpunt.

Wageningen, December 1947.

De Secretaresse van de
Phytopathologische Commissie,
Caroline H. Klinkenberg.

VERSLAG van de Commissie voor de Plantenphysiologie over het jaar 1947.

In dit jaar werden twee bijeenkomsten georganiseerd. De eerste vond plaats op 15 Maart in het Botanisch Laboratorium te Leiden; sprekers waren Prof. Dr T. H. van den Honert over „De opname van phosphaat door plantenwortels" en Dr M. H. van Raalte over „Samenstelling van de lucht in de luchtkanalen van rijstwortels".

De tweede bijeenkomst werd gehouden 29 November in het Botanisch Laboratorium te Amsterdam. Als spreker trad op Dr L. K. Wiersum, die het „Permeabiliteitsonderzoek van wortelweefsel in verband met het opname-probleem" behandelde.

Beide bijeenkomsten werden goed bezocht.

Door loting werd de volgorde van aftreden van de leden van de en Mej. A. L. van Beverwijk: Indrukken van Engelse laboratoria;

Commissie als volgt vastgesteld: Mej. Dr A. KLEINHOONTE 1948; Dr A. W. H. VAN HERK 1949; Dr W. H. ARISZ 1950; Dr V. J. KONINGSBERGER 1951; Mej. Dr A. M. HARTSEMA 1952; Dr J. W. M. ROODENBURG 1953; Dr T. H. VAN DEN HONERT 1954.

De Secretaris,
Amsterdam, December 1947. A. W. H. VAN HERK.

VERSLAG van de Commissie voor Plantensystematiek en -geografie over 1947.

Nadat in een eerste bespreking op 16 November 1946 te Utrecht de Commissieleden de functies onderling verdeeld en het karakter dat men de vergaderingen wilde doen hebben bepaald hadden, werd de eerste bijeenkomst gehouden op Zaterdag 25 October 1947 in het Botanisch Laboratorium te Utrecht. De belangstelling was zeer bevredigend; er waren 25 aanwezigen.

Aan de Algemene Vergadering zal Dr J. HEIMANS worden voorgesteld ter vervanging van het aftredende Commissielid Dr A. A. PULLE (voorz.).

Dr LANJOUW deed mededeling over de plannen voor het organiseren van een congres van systematici, te houden in Nederland en met beperkt aantal deelnemers, met het doel een vóór-contact tot stand te brengen vóór het Botanisch Congres van 1950 in Zweden.

Korte voordrachten werden vervolgens gehouden door R. A. MAAS GEESTERANUS over de verspreiding van *Cetraria* in ons land; Dr H. J. LAM over Ontwikkelingslijnen bij Pteridophyten en Gymnospermen; Dr A. A. PULLE over de nomenclatuur van *Ginkgo*. Aan het slot van deze voordrachten werden door verschillende aanwezigen vragen gesteld.

Groningen, 14 November 1947. De Secretaresse,
CH. H. ANDREAS.

NOTULEN over 1947.

JAARVERGADERING op Zondag 9 Februari 1947 in de Hortus Botanicus te Amsterdam.

Er zijn aanwezig 2 introducé's, nl. de heren P. v. D. LEEDEN en E. AGSTERIBBE en 65 leden, nl. de dames en heren: ARISZ, ADRIANI, ANDREAS, P. J. BELS, BELS-KONING, A. J. BIANCHI, BLOEMBERGEN, VAN ASPEREN DE BOER, BOK, BOTTELIER, G. BRINK, R. BRINK, H. G. L. DE BRUYN, CROOCKEWIT, DONK, W. VAN DIJK, A. GORTER,

I. DE HAAN, HEIMANS, VAN HERK, HOMBURG, TEN HOUTEN, 'S JACOB, P. JANSEN, JONKER, KARSTENS, KERLING, KLOOS, KONINGSBERGER, G. KRUSEMAN, VAN DER LAAN, LANJOUW, DE LEEUW, J. C. LINDEMAN, MARGADANT, MELTZER, MOOI, F. M. MULLER, NIEKERK-BLOM, OORT, VAN OOSTEN, VAN OOSTSTROOM, DE BRUYN OUBOTER, V. D. PAAUW, A. PFÄLTZER, PIET, PRELL, QUISPEL, ROODENBURG, RIJVEN, SLOFF, VAN SLOGTEREN, STOMPS, THUNG, VERHOEF, P. VERMEULEN, WASSINK, WEEVERS, WENT, WESTHOFF, WIERSUM, J. H. VAN WIJK, R. V. D. WIJK, DE ZEEUW, ZEIJLEMAKER.

Als gevolg van de kolennood is de zaal slechts zeer matig verwarmd, zodat de meeste leden en het Bestuur in jassen gedoken zitten.

Om 10.45 opent de Voorzitter Dr W. H. ARISZ de vergadering. Zijn welkomstwoord richt hij in het bizonder tot Dr P. V. D. LEEDEN, die als Voorzitter van het Verbond van Wetenschappelijke Onderzoekers aanwezig is om een lezing te houden over doel en streven van het Verbond.

De Voorzitter vermeldt met voldoening de opleving in de Vereniging in 1946 na de gedeeltelijke stilstand gedurende de laatste oorlogsjaren: er zijn 2 commissies bijgekomen.

Het heeft in 1946 echter ook niet aan teleurstellingen ontbroken; de tijdschriften hebben nog steeds niet kunnen verschijnen. Thans is de uitgave echter werkelijk binnen korte tijd te verwachten. De wens omtrent een ander, moderner formaat der tijdschriften wordt in de redactiecommissies overwogen.

Zeer kort geleden, in de maand December van 1946, heeft de Vereniging 2 grote verliezen te betreuren gehad door het overlijden van de heren Dr G. L. FUNKE en Dr J. J. SMITH.

Prof. FUNKE was een zeer belangstellend lid, die vaak voordrachten over zijn werk hield, Dr SMITH heeft zonder volledige academische opleiding zeer belangrijk systematisch en organisatorisch werk gedaan in Buitenzorg, waarvoor hij 10 jaar geleden in de feestbundel van Blumea reeds geëerd werd.

Namens de Vereniging spreekt de Voorzitter zijn leedwezen uit over het feit, dat Dr VAN OOSTSTROOM om gezondheidsredenen genoodzaakt is het 1ste secretariaat neer te leggen, 3 jaar voordat zijn mandaat is afgelopen. Hij dankt hem voor alles wat hij voor de Vereniging gedaan heeft en tevens Dr VAN HERK, die de laatste maanden het 1ste secretariaat waarnam.

Ten aanzien van Indië spreekt de Voorzitter de hoop en het vertrouwen uit, dat de situatie langzamerhand zal opklaren. Buitenzorg is thans weer in handen van bevoegde autoriteiten.

Na voorlezing en goedkeuring der notulen van de vorige vergadering volgt het ontwerp-jaarverslag van de 1ste secretaris, de ontwerp-jaarverslagen der permanente Commissies en het Verslag omtrent de Flora Neerlandica. Alle verslagen worden goedgekeurd. De Penningmeester toont zich bij het uitbrengen van 't verslag over de finantiën der Vereniging nogal somber. Dr KONINGSBERGER vermoedt dat deze sombere stemming slechts de toekomst kan gelden, daar alle verliessaldi toch kleiner zijn dan het koersverschil.

Dr JANSEN wijst er echter op, dat hij over een reserve moet kunnen beschikken om de tijdschriften te betalen als deze verschijnen, waarop Dr KONINGSBERGER constateert dat de tijdschriften dus op het ogenblik de grote moeilijkheid vormen; hij stelt voor, de laboratoria te verzoeken hun bijdragen te verhogen, hetgeen zal geschieden. Vervolgens wordt de begroting voor 1947 goedgekeurd.

In de Commissie tot het nazien van de rekening en verantwoording en de bescheiden van de Penningmeester over 1946 worden benoemd de heren D. PIET en H. H. PRELL.

Alle aspirant-leden, die op het convocatiebiljet voorkomen worden bij acclamatie benoemd. Bovendien nog de heren J. G. DE BRUYN, voorgesteld door de leden HARMSEN, SCHEYGROND en D. M. DE VRIES; J. ENGELEN, voorgesteld door de leden HEIMANS, KLOOS en G. KRUSEMAN; BECKER en BOETS, voorgesteld door de leden HEIMANS, VAN HERK en QUISPEL en mejuffrouw D. STAPEL, voorgesteld door het Bestuur.

Alle vacatures in de permanente Commissies worden vervuld op de wijze, zoals voorgesteld op het convocatiebiljet.

Over de benoeming der beide bestuursleden wordt met briefjes gestemd. In de vacature-Dr ARISZ worden uitgebracht 62 stemmen; op Dr J. LANJOUW 43, op Dr W. K. H. KARSTENS 17, blanco 2. In de vacature Dr S. J. VAN OOSTSTROOM worden uitgebracht 62 stemmen; op Dr J. HEIMANS 45, op Dr E. C. WASSINK 13. Van onwaarde 1, blanco 3. Benoemd zijn dus Dr J. LANJOUW en Dr J. HEIMANS.

Daar het reeds over 12 uur is stelt de voorzitter voor de behandeling der statutenwijzigingen uit te stellen tot de namiddagvergadering en thans het woordt te geven aan Dr P. VAN DER LEEDEN, Voorzitter van het Verbond van Wetenschappelijke Onderzoekers, om zijn lezing te houden over doel en betekenis van het Verbond.

Dr VAN DER LEEDEN spreekt over: *Wetenschap en Maatschappij.*

De beoefenaars der wetenschap hebben de laatste eeuwen merkwaardig ver buiten het gewone maatschappelijke leven gestaan, zoals dit zich uit in sociaal en politiek opzicht.

In de 19de eeuw begon de industrie wetenschappelijke vondsten voor het eerst uit te buiten; sedert dien is het inzicht in de waarde van de wetenschap voor de industrie steeds toegenomen. Deze laat daarom meer en meer wetenschappelijk onderzoek op uitgebreide basis uitvoeren. Door zijn acommerciële houding vindt de wetenschapsmens hiervoor vaak niet de adequate materiële beloning. Ook in andere werkkringen is dit het geval.

Het Verbond van Wetenschappelijke Onderzoekers wil echter niet in de eerste plaats ijveren voor verbetering van de maatschappelijke positie der wetenschaps-beoefenaars. Het beschouwt dit ondergeschikt aan het hoofddoel; hoewel het de aandacht wenst te vestigen op de noodzakelijkheid de onderzoekers een positie te verschaffen, die hen in staat stelt zich volledig en onbezorgd aan hun taak te wijden.

Het Verbond ziet zijn hoofdtaak hierin: de wetenschappelijke onderzoekers bewust te doen worden van hun maatschappelijke verantwoordelijkheid.

Zelden of nooit worden de, soms zeer ver strekkende, sociale en politieke gevolgen van een wetenschappelijke ontdekking voorzien; de ontdekker staat maar zelden stil bij dit probleem. Is het zuiver wetenschappelijk werk gedaan, dan geeft de onderzoeker de vruchten hiervan uit handen, waarna handel en politiek er zich meester van maken. Het ergst is dit wanneer aan de ontdekker door een kleine groep geïnteresseerden geheimhouding is opgelegd.

De wetenschaps-beoefenaars dienen zich af te vragen, welke mogelijkheden er voor de maatschappij bestaan of ontwikkeld kunnen worden, met de stand der huidige kennis. Hiervoor is meer onderling contact nodig — ook internationaal — tussen de vertegenwoordigers van alle takken der wetenschap.

Ook is nauwer contact nodig met het gehele volk; het is de volksvertegenwoordiging, die de credieten voor wetenschappelijk onderzoek moet geven.

Meer en meer blijkt, dat de politici het niet zonder uitgebreide hulp van wetenschappelijke zijde kunnen stellen. Een goede samenwerking kan echter nooit ontstaan, als politici en wetenschapsmensen niet iets van elkaars gebied begrijpen.

Het is een klemmende eis des tijds, dat de wetenschaps-beoefenaar, naast goed specialist, een brede basis van algemeen wetenschappelijk en maatschappelijk inzicht heeft.

Spreker wijst op de moeilijkheden, die zich voordoen bij een streven als dit; deze zijn het gevolg van de specifieke eigenschappen der wetenschappelijke mensen in het algemeen. De Nederlandse geaardheid brengt hierbij nog weer zijn eigen problemen mede.

Als eerste concreet resultaat van het streven van het Verbond noemt spreker het verband met zusterverenigingen in andere landen;

het Nederlands Verbond is lid van de „World Federation of Scientific Workers".

Om 12.45 wordt de vergadering geschorst voor het gebruik van de lunch; waarop om 14.45 de heropening volgt.

Thans zijn volgens de presentielijst aanwezig 5 introducé's, nl. de heren: L. W. JANSEN, E. V. D. LAAN, J. V. D. PLOEG, J. G. N. V. D. WANT, R. J. DE WIT en 56 leden. Er bij gekomen zijn de dames en heren: BADENHUIZEN, A. VAN BEVERWIJK, I. DE BOER, J. VAN DIJK, W. VAN ITERSON, B. DE JONG, KAMERBEEK, LÖHNIS, MARIS MC ARTHUR-HESPE, SCHOTSMAN, KAARS SIJPESTEYN, V. D. VEEN, J. H. DE VRIES, V. DE VRIES, VAN DER WERFF.

De huishoudelijke vergadering wordt voortgezet met de behandeling der voorstellen tot statutenwijzigingen.

Zonder discussie worden aangenomen de wijzigingen in art. 12, 23, 28, en later ook van art. 54 en 55. In art. 33 (nieuw) wordt het woord „bespreking" waar het de eerste maal voorkomt vervangen door „vergadering".

De Voorzitter noemt naar aanleiding van art. 33 (oud) de overwegingen van het Bestuur, die geleid hebben tot het voorstel voor wijzigingen. Door de nieuwe redactie van het artikel wordt de mogelijkheid geopend om als contribuant toe te treden tot de Commissie voor de Phypathologie. Het geldt hier een proef en zal voorlopig slechts voor deze Commissie worden toegepast.

Dr WEEVERS heeft bezwaren; hij vreest een desintegratie van de Vereniging. Dr 's JACOB, Voorzitter van de Commissie voor de Phypathologie zet de redenen uiteen, waarom juist deze Commissie om een nieuwe regeling gevraagd heeft. Een en ander is uitvoerig opgenomen in de notulen van de vergadering van 19 Nov. 1946 van het Bestuur met de Voorzitters en Secretarissen der Commissies.

Op verzoek van Prof. WESTERDIJK legt Dr G. KRUSEMAN uit, hoe de regeling in de Sectie van Toegepaste Entomologie van de Entomologische Vereniging bevalt. Hoewel Dr KRUSEMAN zelf geen voorstander van het systeem is moet hij erkennen, dat het in de praktijk zeer goed voldoet.

De Voorzitter beantwoordt nog enkele vragen omtrent de rechten die deze contribuanten krijgen of liever gezegd: niet krijgen. Dr DONK doet een zeer nuttige stylistische verbetering van het gewijzigde artikel aan de hand. Aldus wordt het aangenomen.

Over de wijziging van art. 44 en 50 (beide oud) inhoudende de contributieverhogingen en de prijs van het N.K.A. wordt vrij veel van gedachten gewisseld. De heer ZEYLEMAKER wenst de contributie op de oorspronkelijke hoogte te houden, maar het N.K.A.

duurder te maken; de heer **Adriani** stelt een contributie volgens salarisgroepen voor en Dr **Quispel** een geheel progressieve contributieregeling, zoals bij de Chemische Vereniging. De heer **Gorter** wil als bezuinigingsmaatregel de publicaties in het Recueil drastisch bekorten. Dr **Arisz** zegt, dat dit in de Redactie-Commissie reeds overwogen wordt en dat er al een vaste grens gesteld is. De heer **Prell** vraagt of het niet beter is de contributie op *f* 15.— te brengen en het N.K.A. gratis te blijven verstrekken. Volgens de Penningmeester zou dit inderdaad de beste oplossing zijn. Men vindt de verhoging met *f* 5.— echter een wat al te krasse maatregel. Daarom verzoekt de Voorzitter het Bestuursvoorstel aan te nemen voor één proefjaar. Aldus geschiedt.

Tenslotte kon met een uur vertraging worden overgegaan tot de Wetenschappelijke Vergadering.

De Heer V. **Westhoff** spreekt over:

Het associatie-begrip in geografisch verband.

Besproken wordt het verschijnsel, dat vele plantengezelschappen evenals bepaalde planten- en vele diersoorten van de ene landstreek naar de andere min of meer geleidelijk van kenmerken veranderen: hun qualitatieve en quantitatieve soortencombinatie vertoont regionale verschillen, meestal met continue overgangen, bij een geografisch hiaat met discontinue. De meer algemene term „plantengezelschap" (phytocoenose) houdt behalve het empirische uitgangspunt der phytosociologie (de regelmatige ruimtelijke groepering der plantenindividuen naar soorten en levensvormen) ook de hypothese in, dat sociale binding tussen planten bestaat. Aangetoond wordt dat deze binding inderdaad als het criterium van een phytocoenose moet worden beschouwd (Russische onderzoekers). Het oorzakencomplex van de samenstelling ener phytocoenose bestaat uit 1. de tegenwoordige milieufactoren, 2. de relaties tussen de componenten voortvloeiende uit hun specifieke eigenschappen, 3. historisch-geografische factoren. Een phytocoenose is de resultante van een langdurig proces van selectie en wederzijdse aanpassing, zij heeft een zekere individualiteit. Bij laag georganiseerde gezelschappen zijn de edaphische en microklimaatfactoren beslissend, bij hoger georganiseerde komt het macroklimaat in soortencombinatie en structuur steeds meer tot uiting. In overeenstemming hiermee blijkt nu, dat de geografische differentiatie der associaties toeneemt naarmate zij op een hogere trap van ontwikkeling staan. Zo blijken waterplanten- en oeverassociaties (*Potamion, Phragmition*) althans binnen een groot deel van Europa geen geografische differentiatie te vertonen: het microklimaat van water is over grote arealen meer homogeen dan dat van land. Land-pionierassociaties zijn geografisch reeds in geringe mate gedifferentieerd. Bij het *Elymeto-Ammophiletum* langs de Atlantische en Baltische kusten blijkt van Z. naar N. een geleidelijke verschuiving in de floristische samenstelling; de arealen der componenten zijn nog te weinig gecorreleerd om de onderscheiding van geografische varianten (althans op deze grondslag) mogelijk te maken, waarin de nog geringe mate van onderlinge binding tot uiting komt. Binnen het *Cicendietum filiformis* zijn van Gascogne tot Holstein reeds geografische varianten aantoonbaar. Bij hoger georganiseerde verbonden (*Corynephorion*, *Molinion*, *Caricetalia fuscae*) kan men reeds duidelijk vicariërende associaties onderscheiden, b.v. het (*Eu*-) *Molinietum* in Midden-Europa en het *Cirsieto-Molinietum* in Nederland tot in Noord-Frankrijk. Dit laatste is tevens een voorbeeld van het verschijnsel, dat bepaalde plantensoorten zowel als associaties in Midden-Europa basiphiel, in het Atlantische gebied indifferent of acidophiel zijn. Bij de structureel hoogst georganiseerde associaties, dwergstruikheiden en bossen, is de geografische differentiatie het verst voortgeschreden; men kan b.v. in het *Calluneto-Genistetum* en *Querceto-Betuletum* binnen Nederland geografische varianten onderscheiden, die ± corresponderen met de plantengeografische districten van VAN SOEST.

Aanvankelijk beschreef men locale vegetatie-eenheden als associaties, zonder veel acht te slaan op die in aangrenzende gebieden. De termen „subassociatie" en „variant" werden zowel voor geografische vicariërende eenheden gebezigd als voor naast elkaar levende edaphische vormen, evenals in de soortssystematiek. Naarmate het onderzoek vorderde, werd het associatiebegrip beperkter en werd regionale coördinatie nodig.

Uiteengezet wordt, waarom het in het wezen der plantensociologische methodiek ligt opgesloten, dat de locaal vastgestelde associatie of sociatie de bouwsteen van de vegetatiebeschrijving moet blijven (DE LEEUW). Voor een oplossing van de systematiek der geografisch vicariërende eenheden is vergelijking met de zoölogische systematiek (KLEINSCHMIDT, RENSCH) nuttig. Besproken wordt daarom het optreden van geografische rassen in het dierenrijk en hun verzameleenheid „Rassenkreis"; de vraag wordt beantwoord, waarom dit verschijnsel zowel in de zoösystematiek als in de synsystematiek, veel minder daarentegen in de botanische idiosystematiek van belangs is: in de laatste o.m. verdoezeling of onwerkzaam maken van het geografisch variëren door grote interfertiliteit van soorten, groot disseminatievermogen en sterke oecotypische differentiatie. In de phytosociologie kan alleen de laatste factor het verschijnsel der geografische differentiatie onwerkzaam maken; dit kan men ondervangen door een juiste keuze van differentiërende soorten (critiek op TÜXEN en KNAPP). Er is dus een analogie tussen zoölogie en phytosociologie. Verschil: „Rassenkreis" is een reële eenheid, de phytosociologische verzameleenheid een typologisch (formeel) begrip. Niet alleen om methodische (zie boven) doch ook om principiële redenen is het dus beter, in de systematiek (in tegenstelling tot de zoölogie) het zwaartepunt te leggen op de locale associatie en niet op de verzameleenheid. Deze laatste noeme men „associatie-groep" of „collectief-associatie"; bij duidelijk verschil in karakteristieke soortencombinatie spreke men voorts van vicariërende associaties, anders van geografische varianten.

Tot slot wordt er de aandacht op gevestigd, dat de studie der geografische differentiatie van plantengezelschappen de kloof overbrugt tussen de resultaten van de op minutieuze analyse berustende „micro-methode" der plantensociologie en de oppervlakkiger „macro-methode" der physiognomische formatiekunde.

Deze voordracht duurde tot 16.30 waarna Dr THUNG een voordracht hield over:

Enkele resultaten der electronen-microscopie bij het virus-onderzoek.

Sinds de eerste studies, o.a. van IWANOFSKI, BEIJERINCK, LOEFFLER en FROSCH aan het einde der vorige eeuw, zijn bij het onderzoek der filtreerbare smetstoffen vele nieuwe methoden toegepast. Naast de filtraties met filterkaarsen, zijn die met collodium-membranen van bekende poriëngrootte in zwang gekomen. Daarnaast zijn physische en chemische bepalingen gedaan, is de ultracentrifuge gebruikt en heeft men electrophorese en serologie toegepast. Thans is de electronen-microscopie bij het virus-onderzoek betrokken. Zij heeft bevestiging gegeven van de vondsten der andere methoden en daarnaast nieuwe feiten aan het licht gebracht.

De vorm van de smetstof van het tabaksmozaïek is afhankelijk van de methoden van isolatie; de agglutinatie met antiserum is specifiek; er bestaat een wiskundige regelmaat van rangschikking der moleculen van het Bushy-stunt — en het Southern-bean-mosaic-virus; de mozaïek-smetstof komt binnen de chloroplasten der zieke planten voor. Al deze verschijnselen waren reeds aangetoond met andere methoden; door de electronen-microscopie zijn zij bevestigd en in beeld gebracht. Nieuwe vondsten zijn: de spermatozoid-achtige vorm van de bacteriophaag van *Escherichia coli* met granulaire tekeningen in de kop; de granulaire lichaampjes in het pokken-virus;

de nucleoiden-achtige lichamen in *Sarcina flava*. Zo heeft het electronen-microscoop meer differentiatie gebracht in de, tot nu toe, meer als eenheid beschouwde wereld der viren.

Nieuwe onderzoekingen door middel der electronen-microscopie, waarbij vooral de aandacht wordt bepaald op de physiologie der zieke plant, zijn door spreker geprojecteerd.

Op het Microbiologisch congres te Leeds in Juli 1946 werd door vooraanstaande virologen het probleem behandeld: „Heterogenesis and the origin of viruses", waarbij verschillende hypothesen werden gelanceerd. De onderzoekers van de viren van het dierenrijk waren van mening, dat deze viren het best zijn te beschouwen als „degraded bacteria", welke hun ingewikkelde eigenschappen, zowel wat betreft structuur als biochemische functies, langzamerhand hebben verloren door gewenning aan een gespecialiseerd parasitisme. De woorden van LAIDLAW zijn in dit verband wel kenmerkend, nl. dat viren zijn: . . . „inert and in a state of suspended animation; within the correct cell however, they would have all the substances required for growth . . . ." en verder: . . . . „They live a borrowed life". De viren worden door hen als organismen beschouwd. De sprekers over plantenviren achtten het echter nog niet de tijd om tot een uitspraak te komen over het wezen der smetstoffen. Daarvoor is het aantal der goed onderzochte viren nog te klein, nl. ongeveer 5% der bekende plantenviren. Een definitief antwoord op bovengenoemde hypothesen is thans ook met het electronen-microscoop nog niet te geven.

Om 17.15 sloot de voorzitter de vergadering.

LEDENVERGADERING en excursie naar de Noord-Oostpolder, op Vrijdag 11 en Zaterdag 12 Juli 1947.

In een striemende regen en met felle wind reden op Vrijdagavond 11 Juli 1947 twee autobussen met leden der Vereniging de verlatenheid van de Noord-Oostpolder binnen. De verlatenheid bleek echter een vergissing van de eerste indruk te zijn. In de warme cantine te Emmeloord met de kopjes koffie met koek van de Heer BEKEBREDE ontstond direct een prettige en gezellige sfeer, die de gehele vergadering en excursie verder kenmerkte.

Om 20.30 opende de Voorzitter Dr W. H. ARISZ de vergadering. Enkele van onze gastheren waren aanwezig als introducé's op de vergadering, nl. de heren van de Afdeling Onderzoek van de Directie van de Wieringermeer (Noord-Oostpolder-werken): Dr A. J.

Zuur en de Heer W. Betzema. Verder was als introducé aanwezig Mejuffrouw K. Kristensen, chemica uit Zweden. 50 leden namen aan de vergadering en excursie deel, nl. de dames en heren: Alberda, Arisz, van Asperen de Boer, Bels-Koning, Bennema, D. Bakker, A. T. J. Bianchi, F. Bianchi, Bottelier, W. E. G. de Bruin, H. G. L. de Bruyn, Bremer, Bremer-Reinders, A. C. Boer, Casparé, Drion, Duijm, A. Gorter, C. J. Gorter, Hartsema, Heimans, Hof, van Hell, van den Honert, C. Th. A. de Jong, Kaars Sijpestein, Kleinhoonte, Lam, Lanjouw, F. M. Muller, Oomen, Oortwijn Botjes, ter Pelkwijk, Pool, Roest, Ruys, van Schreven, Sloff, Spierenburg, van Soest, Tjallingii, V. de Vries, van Waesberghe, Wagenaar Hummelinck, Walenkamp, Weevers, Went, R. v. d. Wijk, Bloembergen, Mennega, van Rij, Feekes.

Voor de huishoudelijke vergadering was niets bizonders aan de orde. Na voorlezing en goedkeuring der notulen van de vorige vergadering volgde de benoeming bij acclamatie van de aspirant leden; 1. die, welke voorkomen op het convocatie-biljet; 2. enige op de vergadering voorgestelde personen, nl. Mevrouw R. C. Reinders-Corbach, voorgesteld door de leden: v. d. Honert, Karstens, en Walenkamp; de heren A. T. G. Slootweg, voorgesteld door de leden v. Ooststroom, Koster en Maas Geesteranus; A. J. Hijner, voorgesteld door de leden Lanjouw, Jonker en A. Gorter, benevens een aantal aspirant-gecombineerde-leden met de Ned. Dierk. Vereniging, voorgesteld door het Bestuur. De Voorzitter doet nog enige optimistische mededelingen over de tijdschriften; deze schijnen nu werkelijk binnenkort te verschijnen.

Hierna ging men over tot het wetenschappelijk gedeelte. Dr Ir A. J. Zuur gaf in een zeer interessante voordracht een overzicht van het vele en veelomvattende werk, dat door de afdeling onderzoek van de N. O.-polderwerken gedaan wordt.

Dr W. Feekes sprak over: „De ontwikkeling van de wilde begroeiing van de N.O.-polder in de jaren 1941-1947.

Een levendige discussie volgde over de mogelijkheden van aanvoer der onkruidplanten.

Om 10.30 sloot de Voorzitter de vergadering.

Na een uitstekende nacht in de luxe barakken van het arbeiderskamp Emmeloord werd om 6 uur reveille gehouden. Precies 7 uur vertrok men per auto via Ens en Schokland naar Nagele, waar het gezelschap overstapte op een motor-praam. Onderweg ging men nog aan de wal om de uitgestrekte velden met onkruidplanten en de grote rietbossen te bezichtigen. Om 12 uur volgde een warme lunch te Emmeloord. Evenals het ontbijt was deze lunch samengesteld uit producten van het nieuw ontgonnen land, van buitengewone kwaliteit. Tijdens de maaltijd gaf mejuffrouw TER PELKWIJK een takje met bessen van *Vaccinium corymbosum* door, „zo groot als kleine druiven”!.

Daar het gezelschap hier voor het laatst geheel bij elkaar was, nam de voorzitter de gelegenheid te baat om de gastheren, de Directie van de Wieringermeer (Noord-Oostpolder-werken) met name de heren FEEKES, ZUUR, BOER, BAKKER, BETZEMA en TUININGA, van harte dank te zeggen over de bizondere ontvangst en de leiding bij de gehouden en nog te houden excursies. De heer BEKEBREDE, hoofd van de cantine, met zijn helpers dankte de Voorzitter voor de uitstekende materiële verzorging.

Des namiddags werd nog een autobus-tocht door de polder gemaakt, via Luttelgeest, Marknesse tot dicht bij Vollenhove. Deze tocht ging door het reeds ontgonnen deel van de polder. Proefvelden voor onkruidbestrijding en een ontginningsboerderij werden bezocht met proefvelden over vruchtwisseling. Dit laatste bezoek nam zoveel tijd in beslag, dat de bezichtiging van de proef-bebossing moest vervallen. Via Ramspol verlieten wij de polder en werden te half zes op het stationsplein te Zwolle afgezet.

LEDENVERGADERING op Zaterdag 25 October 1947 om 19.30 uur, in het Botanisch Laboratorium te Utrecht Lange Nieuwstraat 106.

Volgens de presentielijst zijn aanwezig 23 introducé’s — waaronder leden van de Nederlandse Plantenziektekundige Vereniging en van de Nederlandse Mycologische Vereniging; nl. de dames en heren: E. J. VAN BEUSEKOM, J. G. VAN DEN BERGH, K. DIKSTAAL, P. GOEDHEER, J. J. HERINGA, N. P. JANSEN, J. H. KAUFMANN, D. VAN DER LAAN-SOUTENDIJK, M. VAN MESDAG, M. T. VAN MESDAG-SPIRY, T. M. M. OORT-VAN MESDAG, L. E. VAN ’T SANT, G. VAN DER STADT, R. N. DE VRIES, J. DE WAARD, C. WIERSUM-VAN THIENEN, V. WITT, M. C. J. ZEIJLEMAKER-BON en 5 onleesbaar.

Voorts 80 leden: de dames en heren: ANDREAS, ANKER, ARISZ, BARKMAN, G. F. J. BECKER, BELS-KONING, VAN BEVERWIJK, A. J. BIANCHI, S. DE BOER, BOK, BOTTELIER, BAKHUIZEN VAN DEN BRINK, COSQUINO DE BUSSY, CASPARÉ, DERX, DRIJVER, DEN DULK, P. A. FLORSCHÜTZ, MAAS GEESTERANUS, A. GORTER, HEIMANS, VAN HERK, VAN DEN HONERT, HOOGLAND, TEN HOUTEN, HOUWINK, ’S JACOB, P. JANSEN, JONKER, JONKER-VERHOEF, KARSTENS, KLOOS, VAN DER

Kloot, Koningsberger, Koster, Koster-Bouman, J. Kuyper, van der Laan, Lam, Lanjouw, Docters van Leeuwen, J. C. Lindeman, Margadant, Mennega, Meyer, Montagne, Mooi, Mulder, Niekerk-Blom, Nieuwenhuijsen, Oomen, Oort, van Ooststroom, de Bruyn Ouboter, J. W. Pfaeltzer, Polak, Prell, Pulle, A. F. M. Reijnders, Roodenburg, Scheygrond, Schotsman, Smulders, Spierenburg, van der Steen, Thung, van der Veen, P. Vermeulen, G. A. de Vries, Vroman, Wassink, Weevers, Went, Wiersum, de Wilde, R. van der Wijk, Zeijlemaker en 2 onleesbaar.

Met het oog op de beperkte tijd opent de Voorzitter Dr W. H. Arisz, de vergadering met een zeer kort woord, en heet daarbij de leden van de Ned. Mycologische en van de Ned. Plantenziektenkundige Verenigingen van harte welkom.

De notulen worden gelezen en goedgekeurd. Van de aspirantleden, die op het convocatiebiljet genoemd worden, heeft mejuffrouw L. Berkenbosch zich teruggetrokken. De overigen worden bij acclamatie benoemd. Tijdens de vergadering worden nog voorgesteld: H. J. van Hattum door de leden Lam, Maas Geesteranus, van Ooststroom en A. J. van Tooren door de leden Barkman, Lam, van Ooststroom.

Direct hierna houdt Dr A. J. P. Oort zijn inleiding tot de film over de *Nematoden vangende schimmels.*

Onder de parasitaire schimmels zijn er, die bizondere organen vormen, waarmee zij Nematoden, Amoeben en andere organismen kunnen vangen. De vangapparaten zijn gebouwd volgens twee principes; volgens het ene wordt na contact met de prooi een snel verhardende kleefstof afgescheiden, volgens het andere wordt de prooi gestrikt. Bij de vangapparaten van de eerste groep treft men in het mycelium ringen en lussen aan, die soms tot gehele netten kunnen uitgroeien, in andere gevallen lijmknoppen, terwijl in weer andere gevallen alle hyphen bij contact een kleefstof afscheiden, De strikkende vangapparaten bestaan uit ringen van drie cellen, die aan een kort steeltje met de hoofdhyphen zijn verbonden. De cellen van de ring zetten bij contact plotseling binnenwaarts uit, de val slaat dicht en de prooi wordt geworgd. Daarna dringen hyphen in de prooi binnen en zuigen deze geheel uit.

De vangapparaten worden alleen gevormd bij aanwezigheid van levende Nematoden of een vloeistof, waarin deze een tijdlang verblijf hebben gehouden. Bij koken gaat de activerende werking verloren. De vangapparaten werken min of meer specifiek; er zijn alleen Nematoden vangende schimmels en andere, die alleen Amoeben vangen. Ten gevolge van prikkeling wordt de protoplasmastroming in de cellen van de vangapparaten sterk versneld en gericht naar de geprikkelde plaats.

Na de pauze, waarbij voor het eerst na de oorlog weer thee geschonken wordt, volgt de vertoning van de film „Les champignons prédateurs", die door J. COMANDON en P. DE FONBRUNE van het Institut Pasteur, Annexe de Garches, bij Parijs werd opgenomen. Het is een prachtige film, die de bewegingen der aaltjes en de reacties der schimmels onder het microscoop laat zien. Duidelijk blijkt hierbij, welke grote mogelijkheden de micromanipulator van DE FONBRUNE biedt. Dit instrument staat in de kelder van het Botanisch Laboratorium te Utrecht opgesteld. Dr KONINGSBERGER nodigt belangstellenden uit het na afloop der vergadering te bezichtigen. De „microforge", waarmede naaldjes, pipetjes en mesjes voor de micromanipulaties gemaakt worden is eveneens aanwezig. Beide instrumenten zijn wonderen van vernuft.

1 Februari 1948. De 2de Secretaresse,
H. C. BELS-KONING.

VERSLAG van de Commissie tot het nazien van Rekening en Verantwoording en de bescheiden van de Penningmeester over 1947.

Ondergetekenden hebben op 14 Februari 1948 ten huize van de Penningmeester de rekening en verantwoording van 1947 en de bescheiden van de Penningmeester nagezien. Zij stellen de ledenvergadering voor, de rekening en verantwoording van de Penningmeester goed te keuren en deze te dechargeren onder dankbetuiging voor de vele moeite en zorg, besteed aan het zorgvuldige en voorzichtige beheer der geldmiddelen onzer Vereniging.

S. E. DE JONGH.
J. L. VAN SOEST.

VERLIES EN WINST OVER 1947.

Kok-Ankersmit-Fonds							
Uitgaven	*f*	520	05	Ontvangsten.	*f*	1692	40
Koersverl. en afl.	„	488	—				
Saldo winst	„	684	35				
	f	1692	40		*f*	1692	40
Brumund-fonds							
Uitgaven	*f*	470	10	Ontvangsten.	*f*	2919	50
Koersverl. en afl.	„	3318	25	Saldo verlies	„	868	85
	f	3788	35		*f*	3788	35
Vrije fonds							
Contributie (oninbaar)	*f*	490	—	Contributies.	*f*	5940	55
Onkosten	„	630	27	Interest.	„	179	36
Vergaderingen	„	204	50	Saldo verlies	„	56	54
Lidmaatschappen	„	290	—				
C. v. phytop.	„	26	82				
C. v. floristiek	„	77	48				
C. v. Sociologie	„	5	—				
Z. Z. C.	„	63	89				
Herb. en bibl.	„	962	98				
Recueil	„	1189	90				
Archief	„	2219	61				
Koersverschil	„	16	—				
	f	6176	45		*f*	6176	45

BALANS 1 JANUARI 1948.

Kok-Ankersmit-Fonds.					
Eff. en Hypoth.	*f* 32483	69	Fonds 1-1-'47	*f* 35663	58
Kassaldo	„ 3864	24	Saldo *winst*	„ 684	35
	f 36347	93	Fonds op 1-1-'48	*f* 36347	93
Brumund-fonds					
Effecten	*f* 21140	65	Fonds 1-1-'47	*f* 29256	55
Kassaldo	„ 7247	05	Saldo *verlies*	„ 868	85
	f 28387	70		*f* 28387	70
Vrije fondsen.					
Interest (te innen)	*f* 330	—	Fonds 100-jarig bestaan	*f* 2000	—
Contributie (te innen)	„ 875	—	Fonds Flora Neerlandica	„ 469	55
Debiteuren	„ 23	80	Vrije fonds 1-1-'47 . . *f* 8598,07		
Effecten	„ 4315	83	Saldo *verlies* . . . . . „ 56,54		
Kassaldo	„ 10660	66		*f* 8541	53
	f 16205	29			
Crediteuren	„ 5194	21			
	f 11011	08		*f* 11011	08

BEGROTING 1948.

Kok-Ankersmit-Fonds.

Ontvangsten	f 1000,—	Onkosten	f 25,—
		Herb. en bibl..	„ 300,—
		Biol. Station.	„ 250,—
		Sigma	„ 200,—
		Natuurmonumenten	„ 100,—
		Wahlenb. terrein.	„ 55,—
		Bijschrijven	„ 70,—
			f 1000,—

Brumund-Fonds.

Ontvangsten	f 750,—	Onkosten	f 25,—
		Friske Gea	„ 25,—
		Comm. v. Soc.	„ 50,—
		Comm. W. Flora	„ 50,—
		Z. Z. C..	„ 100,—
		Herb. en bibl.	„ 100,—
		C. v. flor.	„ 100,—
		Ivon	„ 100,—
		Bijschrijven	„ 200,—
			f 750,—

Vrije Fonds.

Contributie	f 5200,—	Recueil	f 3000,—
Interest	„ 200,—	Kr. Arch.	„ 3000,—
Verkoop	„ 1000,—	Herb. en bibl.	„ 500,—
Bijdrage Lab.	„ 1350,—	Onkosten	„ 500,—
		Verg.	„ 200,—
		Comm. v. Phytopath.	„ 50,—
		Comm. v. Physiol..	„ 50,—
		Bur. Schimmelc.	„ 100,—
		Nat. en Gen. Congres.	„ 3,—
		Ned. Phytopath. Ver.	„ 10,—
		Contactcommissie	„ 50,—
		Intern. nat. besch.	„ 50,—
		Station Den Helder	p.m.
		Onvoorzien	„ 237,—
	f 7750,—		f 7750,—

VERSLAGEN OVER HET JAAR 1948.

JAARVERSLAG van de eerste secretaris over 1948.

Het verslagjaar bracht voor de Kon. Ned. Bot. Ver. geen al te schokkende gebeurtenissen mee.

De thans ingegane contributieverhoging heeft nog niet de verbetering in de finantiële positie van de vereniging opgeleverd, die er van was verwacht. Integendeel heeft de penningmeester met grote moeilijkheden te kampen.

Vooral de uitgaven voor onze tijdschriften bereikten een schrikbarende hoogte.

Toch is ook thans nog niet de achterstand in de uitgave der tijdschriften ingehaald.

Van het Recueil des Travaux Botaniques Neérlandais verscheen deel 41 in twee afleveringen met tezamen 540 blz., waarin twee proefschriften en een 7-tal grote en kleinere artikelen van oudere leden werden gepubliceerd.

Deel 56 van het Nederlandsch Kruidkundig Archief met de verslagen over 1944 en 1945 en een aantal artikelen de Nederlandse plantengroei betreffende, dat bestemd en gereed was, om in 1948 te verschijnen, kon door onverwachte moeilijkheden niet verzonden worden.

Van de Flora Neerlandica daarentegen is het eerste deeltje nog juist voor het einde des jaars uitgekomen. Het behandelt op 96 blz. met 44 illustraties de Pteridophyta en Gymnospermae en is voor de leden te bekomen op bestelling bij de penningmeester onder gelijktijdige storting van *f* 3.75 per exemplaar op de giro-rekening (93030) van de vereniging.

Het bestuur vergaderde drie maal en nog een keer met de voorzitters en secretarissen der permanente commissies, zoals voorgeschreven is in de nieuwe Statuten.

De ondervoorzitter was gedurende een groot deel van het jaar afwezig wegens zijn onderzoekingsreis in Suriname.

Algemene ledenvergaderingen werden gehouden op 1 Februari (Jaarvergadering) te Utrecht, op 29 Mei te Groningen en op 23 October wederom te Utrecht.

De zomervergadering was voorafgegaan door een Zaterdagmiddagexcursie naar de Zeyer Strubben en het Bolleveen en werd gevolgd op Zondag 30 Mei door een bezoek aan de Hortus de Wolf te Haren en aan het Anloër diepje en het Lheebroekerzand. Een groot aantal leden nam deel aan deze tochten en allen waren zeer voldaan over het genotene.

Op de Jaarvergadering werd in plaats van de aftredende 2e secretaresse Mevr. BELS-KONING gekozen tot bestuurslid Mej. Dr A. JAARSVELD.

In de Commissie voor Redactie van het Recueil werd Dr L. G. M. BAAS BECKING vervangen door Dr E. C. WASSINK. Verder werden, zover dat toegestaan is, de aftredende commissie-leden herkozen en aan de sub-commissie voor Zuiderzee-onderzoek toegevoegd de heer D. BAKKER. In de comm. e. werden de aftredenden: Ir V. D. KLOOT, Dr DE VRIES en Dr WASSINK vervangen door Dr JONKER, P. R. DEN DULK en H. TJ. WATERBOLK; in de comm. f. Dr DE LEEUW door J. G. SLOFF, in de comm. g. Dr J. C. 'S JACOB door Dr C. WEHLBURG, in de comm. h. Mej. Dr A. KLEINHOONTE door Mej. Dr C. J. GORTER, in de comm. i. Dr PULLE door Dr HEIMANS.

Als redactie van de Flora Neerlandica werden aanvaard WEEVERS als voorz., HEIMANS als secretaris, KLOOS en VAN OOSTSTROOM.

De voorzitter hield een jaarrede, getiteld: „In open Vaarwater", welke in het N. Kruidk. Archief deel 56 is opgenomen. In de middagvergadering spraken Dr PULLE (over de ontwikkeling van het botanisch onderzoek in Suriname) en Dr VERMEULEN (over de splitsing van het geslacht Orchis).

In de zomervergadering sprak Dr F. VAN DER PAUW over de invloed van de watervoorziening op de ontwikkeling en de opbrengst van haver, Dr R. VAN DER WIJK gaf een demonstratie van stereoprojectie en Hortulanus LAARMAN een inleiding tot het bezoek aan de Hortus de Wolf te Haren.

In de Octobervergadering werden voordrachten gehouden door Dr LAM (over Stachyosporie en Phyllosporie als basis voor een Systeem) en Dr A. MANTEN (over Phototaxis van purperbacteriën).

De commissies hielden hun gebruikelijke twee vergaderingen, die bijna zonder uitzondering zeer goed bezocht waren.

Het op al deze commissie-bijeenkomsten verhandelde wordt in de afzonderlijke verslagen vermeld.

Doordat tegenwoordig 10 verschillende instanties in onze vereniging autonoom de leden aanschrijven, is onze administratie wel zeer omslachtig geworden. Om daarin vereenvoudiging en bezuiniging te brengen, wordt het nodig geoordeeld, dat in het vervolg het convoceren voor ledenvergaderingen ook voor die van de commissies uitgaande, geschiedt door het 2e secretariaat.

De voorzitter resp. de eerste secretaris vertegenwoordigden de Vereniging ter gelegenheid van het afscheid van Prof. PULLE en dat van Prof. VAN ITERSON en ter gelegenheid van het 75-jarig Jubileum van het Kon. Ned. Aardrijkskundig Genootschap.

Bij de reorganisatie van de Biologische Raad van Nederland is als vertegenwoordiger van onze vereniging in dat lichaam Prof. LAM benoemd.

In het ruilverkeer van onze tijdschriften met buitenlandse botanische instituten kwam weer enige uitbreiding door opname van instituten te Madrid, Mexico en Trinidad.

Op voorstel van een zeer groot aantal leden ter zomervergadering in Groningen bijeen werd door de ledenvergadering van 23 October in Utrecht Prof. Dr FREY-WYSSLING te Zürich benoemd tot corresponderend lid. De heer FREY-WYSSLING, die juist twintig jaar eerder tijdens zijn werkzaamheid op Java lid van onze vereniging was geweest, heeft deze benoeming met veel genoegen aanvaard.

De overeenkomst met de Nederl. Dierkundige Vereniging is thans zo gewijzigd, dat alleen nog gecombineerde leden een reductie van contributie voor onze vereniging tot *f* 10.— genieten, studentleden betalen in 't vervolg *f* 7.50, onverschillig, of zij ook lid zijn van de N.D.V. Deze reductie vervalt met het doctoraal examen. Evenzo is een nadere regeling getroffen voor de toelating van contribuanten-phytopathologen. Als criterium is gesteld, dat niet worden geaccepteerd degenen, die plantkunde als hoofdvak hebben gestudeerd, die dus geacht kunnen worden in aanmerking te komen als gewoon lid van de K.N.B.V.

Het aantal gewone leden, dat in het begin van dit jaar nog de 500 bereikte vertoont, doordat het aantal afschrijvingen de aanmelding van nieuwe leden nogal aanmerkelijk overtrof, duidelijk een dalende tendens.

Door de dood ontviel ons een lid; Prof. Dr OTTO DE VRIES overleed op 27 Nov. '48 in Den Haag op 67-jarige leeftijd.

Na in Leiden en Zürich chemie te hebben gestudeerd, werd Dr DE VRIES in 1909 scheikundige aan het proefstation voor tabak te Klaten op Java. In 1915 ging hij over naar het Rubberproefstation te Buitenzorg, waarvan hij tot 1930 Directeur was, de laatste jaren tegelijk ook buitengewoon Hoogleraar in Scheikunde aan de Geneeskundige Hogeschool te Batavia. Na repatriëring in 1930 werd Prof. DE VRIES Directeur van het Rijks-Landbouwproefstation voor Akker- en Weidebouw te Groningen en in 1939 Hoofddirecteur van het Rijkslandbouwproefstation en Bodemkundig Instituut. Van 1945 tot z'n dood was hij Voorzitter der Landbouworganisatie T.N.O. en der Landbouwnijverheids-organisatie T.N.O. Op het gebied van de Rubber-chemie had Prof. DE VRIES een internationale naam, zoals blijkt uit een aantal eretitels en hoge onderscheidingen. In 1929 als voorzitter van het IV. Pacific Science Congres werd hij gedecoreerd als Ridder in de Orde van de Nederlandse Leeuw.

Niet alleen van huis uit, als oudste zoon van HUGO DE VRIES, had de chemicus OTTO DE VRIES belangstelling voor botanie, maar in al zijn functies, zowel die op Java, in Groningen als in Den Haag was hij ook ambtelijk bij botanische questies nauw betrokken. Hij was sedert 1 Juni 1912, dus gedurende meer dan 36 jaren, lid van onze vereniging.

J. HEIMANS.

VERSLAG van de Commissie van Redactie van het Recueil des Travaux botaniques néerlandais over 1948.

Gedurende het gehele jaar 1948 was de ondergetekende bezig met het verzorgen van Vol. XLI (1946-1948). In Januari verscheen daarvan de eerste aflevering, groot 212 pagina's, welke bevatte de artikelen van de heren WIERSUM (dissertatie), FUNKE, WEEVERS, STOMPS, JONKER en WASSINK. De 2de afl. verscheen in Juli. Zij loopt tot p. 540 en bevat artikelen van de heren REIJNDERS en STAFLEU (diss.). De 3de afl. is bijna gereed en bevat artikelen van de heren ALBERDA en KREGER (beide dissertaties). Hiermee zal het deel worden afgesloten.

In de samenstelling van de Commissie kwam verandering doordat Prof. BAAS BECKING werd vervangen door Prof. WASSINK, Prof. STOMPS door Prof. VAN HERK.

De secretaris van de Commissie,
Baarn, 31 December 1948. A. A. PULLE.

VERSLAG der Commissie van Redactie voor het Nederlandsch Kruidkundig Archief over 1948.

De Commissie had gehoopt, dat in 1948 althans deel 56 van het Archief zou kunnen worden uitgegeven. Onverwachte moeilijkheden vertraagden helaas op het laatste ogenblik het afdrukken van één der vellen, waardoor het zelfs onmogelijk bleek het deel nog einde December te laten verschijnen. Het zal nu zeer binnenkort in handen van de leden zijn, daar alles voor afdrukken gereed is.

Opgenomen zijn de verslagen over 1944 en 1945 en enige floristische mededelingen. De verslagen over 1946 en '47 en een groot aantal belangrijke artikelen wachten nog steeds op publicatie.

De Secretaris,
Nijmegen, 31 Dec. 1948. J. H. KERN.

VERSLAG van de Commissie voor de Bibliotheek, het Herbarium en het Archief over 1948.

Twee belangrijke verzamelingen werden aan het Herbarium toegevoegd; in Februari stonden de erfgenamen van wijlen JOHAN JANSEN, op wens van de zo betreurde florist, zijn mooie collectie af, tellende 2234 Phanerogamae en 285 Musci. In Maart schonk C. G. G. J. VAN STEENIS zijn Nederlands herbarium, bevattende 2919 Phanerogamae, dat in grote dank werd aanvaard. Verder werd het Herbarium verrijkt met 3 Hepaticae (geschonken door W. MEIJER), 6 Amaranthaceae (Dr Ir A. W. KLOOS), 1 *Linaria spuria* (Dr C. A. BACKER), 1 *Arctostaphylos Uva ursi* (Dr V. WESTHOFF) en 7 Compositae (Ir J. L. VAN SOEST). In totaal nam in 1948 het Herbarium met 5456 nummers toe.

Uit de collecties van de Vereniging werden dit jaar planten uitgeleend aan de volgende personen: W. MEIJER (19 Hepaticae, 5 Musci), Dr G. KRUSEMAN (175 Betulaceae), J. GREMMEN (23 Fungi), Dr W. BEIJERINCK (81 Betulaceae), Dr P. JANSEN (135 Gramineae), Dr Ir A. W. KLOOS (18 Amaranthaceae, 4 Portulacaceae), W. MARGADANT (100 Musci), Dr H. R. HOOGENRAAD (5 Orchidaceae) en Ir J. L. VAN SOEST (69 Compositae). Uit vorige jaren zijn nog bijna 1900 nummers uitgeleend aan verschillende personen.

De Bibliotheek werd door 21 personen bezocht, terwijl 295 werken werden uitgeleend. Als bijlage bij dit verslag komt een lijst der aanwinsten, ongerekend de normale aanvulling der periodieken [1]). Enkele nieuwe ruilverbindingen kwamen tot stand, andere werden hersteld. Als nieuw ontvangen tijdschriften mogen hier worden vermeld:

1. Acta facultatis rerum naturalium Universitatis Carolinae, Praha;
2. Anales del jardin botánico de Madrid;
3. Flora Malesiana Bulletin;
4. The Journal of the Microscopical Society of Victoria, Melbourne;
5. Lavori dell'Instituto Botanico dell'Università di Milano;
6. Publicaties van het Natuurhistorisch Genootschap in Limburg;
7. Publications of the „Natuurwetenschappelijke Studiekring voor Suriname en Curaçao".

Behalve 287 tijdschriftdelen (414 afleveringen) werden 213 boeken en brochures ontvangen, voor een deel van instituten, waarmede ruilverkeer is en voor het overige als schenking door de volgende personen:

Prof. Dr W. H. ARISZ (4 stuks); Dr C. A. BACKER (3); Dr .W BEIJERINCK; Prof. Dr K. B. BOEDIJN; L. COOMANS DE RUITER; W. v. DIJK; Prof. Dr ALFRED ERNST, Zürich (14); Dr MARTHE ERNST-

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[1]) Zie noot op pag. 6. Red.

Schwarzenbach, Zürich (3); Dr K. Fröier, Lund; Dr A. J. M. Garjeanne (2); Guiseppe Gola, Padova; Dr H. de Haan (3); Prof. Dr J. Heimans; Dr P. Jansen (3); Mej. Dr A. Kaars Sijpesteijn; Dr W. K. H. Karstens (2); J. Kern, B. en Th. Reichgelt (2); Dr B. Kok; Dr W. Lüdi, Zollikon; Dr A. Manten; Dr J. C. Mooi; H. C. J. Oomen; Dr J. van Overbeek, Modesto (Cal.); Mevr. Dr C. A. Reinders-Gouwentak (2); Dr M. Sjöwall, Lund; Ir J. L. v. Soest (39); Prof. Dr R. von Sóo, Debrecen; Dr C. G. G. J. v. Steenis (13); Dr J. B. Thomas (2); Dr H. v. Vloten (2); Mej. Dr M. A. de Vries; Prof. Dr Th. Weevers; Prof. Dr Ir S. J. Wellensiek (14); Dr V. Westhoff.

Voorts schonken de volgende instituten boekwerken of brochures: Biophysical Research Group Utrecht-Delft (4 stuks); Boyce Thompson Inst. f. Plant Research, Yonkers U.S.A.; Centraal Instituut v. Landbouwkundig Onderzoek, Wageningen (2); Estaçao Agronómica Nacional, Sacavém; Instituut v. d. Veredeling v. Tuinbouwgewassen, Wageningen; Laboratorium v. Microbiologie, Delft (6); Phytopathologisch Laboratorium, Baarn (2); Rijksherbarium (8); Rijkslandbouwproefstation (10); Techn. Physische Dienst T. H.-T. N. O. (3); Werkgemeenschap v. Wetenschappelijke Organisaties in Nederland (2);

Tenslotte werden 2 werken door aankoop verkregen.

De Secretaris,
Den Haag, 30 December 1948. J. L. van Soest.

VERSLAG van de Commissie voor het Floristisch Onderzoek over 1948.

In 1948 werden 2 vergaderingen te Amsterdam gehouden, die zeer talrijke bezoekers trokken. Van het groot aantal floristische mededelingen zullen de voornaamste aan het Ned. Kr. Archief ter plaatsing worden aangeboden.

De zomerexcursie vond plaats in de omgeving van Rockanje onder leiding van Dr Ir A. W. Kloos, waarbij ons medelid C. Sipkes zich zeer verdienstelijk maakte, door als gids in het interessante duingebied te dienen, dat voor een deel onder zijn toezicht staat.

De Commissie stelt voor in 1949 een excursie te houden in Centraal-Friesland, zo mogelijk in de 2e helft van Augustus.

De Secretaris,
P. Jansen.

VERSLAG van de excursie, gehouden op Voorne 24-29 Juli 1948.

Door onvoorziene omstandigheden plotseling voor de taak gesteld dit verslag op zeer korte termijn in elkaar te zetten, zie ik mij verplicht dit te doen uitsluitend aan de hand van de excursielijsten, mijn eigen vrij summiere aantekeningen en mijn herinneringen die, bijna een jaar oud, nu juist niet meer zo heel vers en scherp omlijnd zijn.

Dank zij de goede zorgen van onze vriend SIPKES vonden wij een onderkomen in „Hotel de Houten Paardjes" van de familie HASELBAG te Rockanje. Het grootste gedeelte van het gezelschap was in het hotel ingekwartierd, enkele leden logeerden bij particulieren in de directe omgeving en een vijftal was in eigen tenten gekampeerd vlak bij het hotel. De maaltijden waren gezamenlijk. Door het grote aantal deelnemers was het logies in het hotel wat primitief; 't was volop zomer en knapjes warm, een levendig muggenverkeer, jachtvermaak, er liep wel eens een zelfopgeblazen luchtmatras leeg, maar 't was genoegelijk en gezellig. Het eten was voortreffelijk en de uitstekende en hartelijke verzorging, die wij van de familie HASELBAG genoten, kan niet genoeg geroemd worden. —

Deelnemers waren: de dames ANDREAS en SCHOTSMAN en de heren BIANCHI Sr en Jr, v. DIJK, JANSEN, DE JONGH, KERN, KLOOS, MEYER, MÖRZER BRUYNS, v. OOSTSTROOM, SIPKES, SLOFF, VERMEULEN, WEEVERS, WESTHOFF en v. D. WIJK.

Zaterdag 24 Juli een gemeenschappelijke tocht door het huishok. Op deze en verscheidene latere tochten was SIPKES onze gids en werden ons *Ophrys apifera*, *Himantoglossum hircinum*, *Herminium monorchis*, *Anacamptis pyramidalis*, *Gymnadenia conopsea*, *Scolopendrium vulgare*, *Primula acaulis* en diverse andere rariteiten gedemonstreerd.

Zondag 25 tocht naar het Nieuwe Water, een prachtig duinterrein met een weelde van *Orchis incarnata*, *latifolia* en *maculata*, *Chlora serotina*, *Sturmia*, *Oenanthe Lachenalii*, *Euphorbia Paralias* enz.

Maandag 26 in drie groepen langs dijken en binnenwegen naar Brielle.

Dinsdag 27 's morgens naar het zuidelijke overgangsterrein van Schor en Duin en 's middags naar een adventiefterrein in de duinen, waar vroeger afval van een meelfabriek was uitgestrooid als fazantenvoer. Hieruit hebben zich o.a. gehandhaafd: *Ornithogalum pyramidale*, *Nasturtium austriacum*, *Salvia verticillata* en *nemorosa*, *Leonurus Cardiaca*, *Anchusa officinalis*, *Centaurea Scabiosa*, *Coronilla varia*.

Woensdag 28 's morgens naar het Kruininger gors en 's middags legden ondergetekende en enkele anderen het af tegen de warmte en hielden siesta; wat de overigen toen uitvoerden weet ik niet.

Donderdag 29. Nog enkele hokjes in de buurt van Nieuw-Hoornaar geïnventariseerd, wat tevens vrijwel het slot van de excursie was.

In het geheel zijn 43 excursielijsten met nog 10 velletjes met losse aantekeningen ingevuld voor de 44 hokjes: P. 3. **32**. 34, 43, **41**. 32, 33, 34, 41, 43, 44, **42**. 11, 12, 14, 22, 23, 24, 31, 32, 33, 34, 42, 43, **43**. 31, **51**. 12, 14, 22, 24, 42, 43, 44, **52**. 11, 12, 14, 21, 22, 23, 41, 42, 43, 44, **61**. 22, **62**. 13, 14, 23, 31, 32.

Gevonden zijn de volgende soorten (de getallen geven aan hoe vaak zij aangeschrapt zijn):

Acer ca 1. Pseudoplat. 3. Ach. m. 32. p. 1. Acor. 1. Aeg. 14. Aeth. 9. Agrim. E. 15. Agrostis a. 31 (f. salina 1.) v. 9. Air. c. 1. Aj. r. 3. Alis. P. 6. r. 1. lanceolata 1. lanc. × P. 1. Allium v. 12 (soms met veel bloemen, wat echter in cultuur niet constant blijkt te zijn) Aln. g. 13. i. 3. Alop. a. 8. b. 3. g. 11. p. 1. Alth. o. 3. Am. blitoides 2. hybr. paniculatus 1. Ammo. a. 8. b. 1. Anac. 1. Anag. a. 20. t. 4. Anch. 1, Anem. n. 1. Ang. 15. Anthem. ar. 1. c. 2. Antho. o. 6. Anthr. s. 29. v. 1. Anthyl. 1. Ape. S. 6. Api. g. 12. Are. 3. 17. Arrh. 28 (var. bulbosus 2.) Art. biennis 1. m. 2. v. 9. Aspara. o. 7. Aspl. R-m 2. T. 1. Aste. T. 13 (f. discoidea 1.) Atri. ho. 1. lat. 26. li. 2. p. 9. Av. fa. 3. fl. 3. prae. 2. sativa 4.

Ball. 2. Bat. d. 2. s. petiveri 1, tric. 4. Bel. 26. Berb. 3. Beru. 5. Betu. 9. Bid. t. 4. Bli. v. 2. Bor. 1. Bras. Na. 1. ni. 1. o. 2. Bri. 6. Bro. ar. 1. h. 1. m. 26. se. 1 .st. 13. Bry. 16. But. 8.

Cak. 3. Calama. E. 12. la. 5. Cale. o. 5. Calli. 2. Calt. 5. Camp. ra . . des 1. Caps. 32. Carda. p. 5. Cardu. c. 1. n. 7. Care. ac . . is 4. ar. 9. can. 1. dista. 4. disti. 6. ex. 1. serotina 1. pulchella. 6. gl. 6. hi. 9. lepo. 2. mu. 6. Otrubae 27. panice. 5. panicu 1. Ps. 3. rip. 2. trin. 4. Timmiana 1. ves. 1. vulg. 4. Carl .1. Centa. Cy. 2. J. 24. Sc. 1. Centu. 2. Ceras. ar. 5. glo. 1. s. 5. te. 4. tr. 27. Cerat. d. 5. Chae. t. 2. Chel. 8. Chen. a. 33. f. 15. g. 2. m. 1. r. 14. Chl. s. 3. Chrysa. i. 14. L. 7. s. 1. Cich. I. 5. Endiv. 1. Cin. p. 1. Cirsi. an. 1. ar. 36. l. 27. p. 9. Coch. d. 2. o. 5. Com. 2. Conva. maj. 1 (culta). Convo. a. 21. sc. 28. So. 1. Corn. sa. 1. Coroni. v. 1. Coryl. a. 1. Coryn. c. 1. Crat. m. 19. Crep. b. 1. v. 26. Cynog. o. 10. Cynos. c. 15.

Dac. 30. Dat. 2. Dau. 16. Dipl. m. 3. t. 2. Dips. s. 3. Dros. r. 1.

Echiu. 1. Elo. 2. Ely. a. 4. Epil. a. 2. h. 9. m. 1. pal. 6. par. 9. Epip. l. 1. p. 10 (fl. albis 2). Eq. a. 17. h. 1. lim. 5. litorale 2. p. 9. v. 2. Erig. a. 3. c. 17. Erio. p. 2. Erod. c. 14. glut. 8. Eryn. c. 18. m. 3. Erys. Ch. 18. Eryt. C. 3. l. 4. p. 5. Eupa. 17. Eupho. Es. 1. ex. 3.

H. 13. Par. 3. Pep. 11. Euphr. Od. 2. o. curta 2. nemorosa 4. Ev. 1.

Fagu. 1. Fes. a. 20. e. 18. g. 2. rub. 23 (dumetorum 4). Frag. v. 2. Frax. 16. Fu. o. 5.

Galeops. T. 6. Galiu. Ap. 18. M. 12. p. 14. u. 7. v. 19. Gent. a. 1. Ger. d. 17. m. 21. pu. 11. Rob. 6. Geu. u. 6. Glauc. l. 2. Glaux 8. Gle. 29. Gly. d. 5. f. 13. m. 3. plic. 4. s. 7. Gna. l-a 1. u. 3.

Hed. 5. Heleo. p. 14. Helianthus tuberosus 4. Hera. 23. persicum 1. Herm. 2. Hiera. laev. 1. Pi. 5. u. 2. Himanthog. 1. Hippo. 12. Hippu. 4. Holc. l. 19. m. 6. Honk. 4. Hor. mu. 21. sativ. 3. se. 17. Hu. 7. Hydroco. 11. Hyo. 3. Hype. pe. 6. q. 2. t. 6. Hypo. r. 12.

Ile. 1. In. c. 3. Ir. ps. 11.

Ja. m. 1. Junc. bu. 13. e. 2. Ge. 9. gl. 11. l. 11. (var. litoralis 1) o. 2. su. 1. sy. 2. tenu. 1.

Koel. albescens. 1.

Lac. m. 1. sc. 1. (f. integrata 1) Lami. al. 30. am. 9. p. 8. Lap. 4. Notha 22. mi. 1. Lathy. pr. 17. t. 2. Lem. g. 1. m. 18. p. 1. t. 13. Leont. a. 24. Leonu. 2. Lepid. D. 2. r. 1. Lept. 2. Lig. 11. Lina. C. 1. m. 4. v. 13. Linu. c. 6. usitat. 2. Lith. o. 3. Litt. 2. Lol. m. 12. p. 34. Lon. P. 5. Lot. c. 21. t. 1. u. 5. Luz. c. 5. m. 1. Lychn. d. 5. Fl. 5. ves. 6. Lycops. 5. Lycopu. 9. Lys. Nu. 8. v. 7. (f. verticillata 1.) Lyt. S. 7.

Malv. r. 2. s. 10. v. 6. Matr. Ch. 23. d. 26. Parth. 1. Med. f. 1. l. 25. ma. 3. s. 13. Melil. alb. 2. ar. 6. Ment. aq. 16. ar. 3. nemor. 1. Meny. 1. Merc. a. 2. Moehr. 7. Myoso. c. 7. h. 3. i. 8. p. 3. s. 1. v. 1. Myrio. s. 10.

Nast. am. 1. austriacum 1. o. 2. p. 2. s. 1. Nu. 1.

Oena. fi. 5. L. 5. Ph. 3. Oenoth. b. 2. L. 1. Onobrychis vic. 1. Onon. r. 2. (fl. albis 1.) s. 13. Onop. 3. Ophi. 1. Ophr. a. 1. Orch. i. 6. l. 4. mac. 2. praeterm. 1. Ornithog. pyramid. 1. Ox. s. 3.

Pan. C-G. 1. Pap. d. 14. R. 21. somnifer. 2. Parn. 6. Pas. 27. Ped. p. 3. s. 1. Phalar. a. 7. Phl. a. 7. p. 24. Phr. 33. Piro. r. 4. Plan. C. 6. l. 33. maj. 34. mar. 4. me. 10. Poa an. 35. n. 1. pr. 23. se. 1. tr. 18. Polygal. v. 3. Polygona. m. 1. o. 4. Polygonu. am. 18. av. 32. B. 1. C. 21. lap. 6. n. 8. Pe. 16. Polypod. 1. Polyst. c. 1. F-m. 3. s. eusp. 2. Pop. a. 3. canad. 1. canesc. 1. n. 1. t. 3. Portulac. ol. 1. Pota. cr. 3. g. 4. mu. 1. n. 3. pec. 12. pu. 3. Potent. ans. 32. arg. 2. rep. 23. T. 5. Prune. 21. Puli. d. 29.

Qu. R. 4.

Ran. ac. 28. b. 1. Fl. 6. L. 1. Ph. 7. r. 27. sce. 22. Raphanu. r. 2. s. 1. Res. lutea 3. luteo. 1. Rha. c. 4. F. 2. Rhina. ma. 4 (ook f. serotina 1) mi 2. Rib. G. 4. r. 1. Rob. 1. Ros. ca. 6. du. 5. pi. 1. ru. 5. s. 1. Rub. cae. 24. spp. 2. Rum. Ac . . sa 19. Ac . . la 5. acutus 1. cong. 12. cr. 31. Hyd. 11. o. 14. p. 2. patientia 1. salicifolius 1. sang. 1. Rup. r. 1.

Sagin. a. 1. n. 7. p. 10. str. 4. Salic. h. 2. Salix al. 24. au. 6. ca. 1. ci. 7. pu. 6. r. 12. vim. 4. Sals. 2. Salv. sy. 1. ve. 1. Samb. n. 26. Samo. 5. Sap. o. 2. Sar. 2. Sax. t. 1. Schoe. n. 2. Scir. co. 2. l. 2. m. 22. pa. 5. ?. se. 1. sy. 1. Ta. 14. Scol. 1. Scro. Ne. 1. no. 3. v. 1. Scut. g. 6. Sed. ac. 7. Bol. 1. Sem. 1. Seneb. c. 14. Senec. eru. 16. J. 19. sy. 6. vi. 9. vu. 30. Set. ve. 1. Sh. 3. Sile. c. 2. i. 1. no. 1. nu. 1. Sin. ar. 14. Sis. A. 6. o. 27. p. 4. S. 4. T. 1. Siu. 3. Sola. D. 12. n. 29. triflorum 3. tuberosum 2. Son. ar. 21. (var. maritima 1) as. 22. o. 27. pal. 1. Sor. a. 2. Spar. r. 5. Spart. Townsend. 4. Spergularia ma. 1. me. 6. sa. 2. Spirae. U. 5. Stach. p. 5. s. 2. Stat. L. 1. Stel. gr. 1. m. 30. u. 1. Stu. 4. Suae. m. 3.. Suc. 1. Sym. o. 18.

Tan. 2. Tar. 32. erythrosp. 1. Tax. 1. Tha. mi. dunense 1. silvatica 1. Thl. ar. 18. Thr. 8. Thym. Cham. 5. Tor. A. 4. Trag. m. 9. po. 1. pr. 7. Trif. ar. 2. fr. 17. h. 8. mi. 18. pra. 33. (ook fl. albis) pro. 6. rep. 37. Trigl. m. 6. p. 8. Trio. 3. Trit. j. 2. j. × l. 1. litorale 5. maritimum 3. lit. × mar. 1. r. 25. sativ. 4. Tus. 13. Typha a. 6. l. 3.

Ulm. c. 11. s. 2. Ur. d. 36. u. 20.

Valeriana d. 4. o. 10. Verba. Schrad. 5. Verbe. 2. Vero. ag. 1. An. 7. (aquatica 1.) ar. 6. Bu. 17. Ch. 2. of. 4. Vib. O. 6. Vic. a. 5. C. 28. hi. 1. se. 2. varia 1. Vio. h. 3. o. 3. Riv. of silv. 1. rupestris arenaria 1. trico. arv. 8. marit. 4.

Zan. 8.

In het geheel 606 soorten en vormen. A. W. Kloos Jr.

BEKNOPT VERSLAG van de Pinksterexcursie in Z.-Limburg 1948.

Deelnemers: v. Dijk, Heimans, Jansen, de Jongh, Kern, Reichgelt en Sloff.

Residentie: Hotel Notten te Meersen.

Aankomst: Vrijdag 14 Mei voor het diner, alleen Kern en Reichgelt komen wat later en maken zelfstandig een wandeling, terwijl de anderen na het diner naar Waterval wandelen door V6. **11.** 32, 23 en 14, bij het verrukkelijke weer genietend van Limburg op z'n mooist. Een niet bloeiende onbekende werd meegenomen en bleek, na kweken in Dordrecht, *Campanula glomerata* te zijn. De Jongh heeft in Maastricht in V5. **28.** 34 *Cheiranthus Cheiri* en *Cystopteris fragilis* gesignaleerd.

Zaterdag 15 Mei: Met trein en bus naar Cadier; vandaar door de Dorreweg naar Trichterberg en Savelsberg tot Rückholt: V6. **31**. 14, 31, 33 en **41**. 11. Sterk verarmde orchideeën-flora, alleen nog veel *Listera ovata* en vrij veel *Platanthera* met rechte, benedenwaarts divergerende helmhokjes, enkele *Ophrys muscifera* en *Orchis maculata*. Veel *Euphorbia amygdaloides* en *Phyteuma nigrum*, waaronder één ex., dat door de bleekblauwe kleur aan een bastaard met *Ph. spicatum* deed denken. V. DIJK ontdekte naast *Ulmus campestris* herhaaldelijk ook *Ulmus montana*.

1ste Pinksterdag. 's Morgens een kleine wandeling langs de Geul in de richting Houthem V6. **11**. 33 en 34 met een stukje boshelling in **21**. 12. Zeer mooie vegetatie van *Myosotis silvatica*. *Lychnis diurna* ook met witte bloemen en een sterk met luis bezette plant, waarvan de bloemen helder groen waren. *Rumex Patientia*. Herhaaldelijk *Anthriscus Cerefolium*. 's Middags tot donker wandeling langs het spoor naar helling van Bunde en over Premmelen en Bunde terug. V6. **11**. 31, 13, 11, T6. **61**. 33 en V5. **18**. 22. *Bidens melanocarpus*, *Rumex Patientia*, *Vicia tenuifolia*. De vroeger zo rijke *Orchis maculata*-vindplaats is omgewerkt en de Orchis zo goed als verdwenen. Daarentegen is de sappige helling nog heel mooi. *Carex pendula* verspreidt zich. *Carex flava* en *demissa* zijn er zeer veel, maar nog wat jong. Over het algemeen zijn we trouwens iets te vroeg om een groot aantal typische Zuid-Limburgse planten voldoende op te merken en te bestuderen. In T6. **61**. 33 wordt *Carex vulpina* als nieuw voor Z. Limburg ontdekt; wel zagen we ook herhaaldelijk *C. Otrubae* - *C. nemorosa*, die vroeger altijd voor *C. vulpina* werd gehouden.

2e Pinksterdag. Met trein en bus naar Eys. Eerst Eyserberg en bos doorzocht V6. **33**. 21 en daarna wandeling langs de lijn naar Simpelfelt. **33**, 24, **24**. 13, 11 en 12. *Senecio Fuchsii* en een breedbladige, behaarde plant die aan *Jaquinianum* doet denken. *Calepina corvini*, *Vicia angustifolia* herhaaldelijk met witte bloemen. *Stellaria media neglecta*, *Onobrychis viciaefolia*, *Barkhausia taraxacifolia* en *foetida*? (de laatste ter kweking meegenomen, de pol bleek ook *Poa compressa* te bevatten). *Astragalus glycyphyllus* langs de spoorlijn. In het Eyserbos alleen een aantal *Orchis*-bladrozetten zonder bloei gezien, ook geen andere Orchidaceeën behalve *Listera* en *Epipactis latifolia*.

Dinsdag 18 Mei. Van station Schin-op-Geul naar het Gerendal gewandeld. V6. **22**. 42, 41 en 43. Aan het begin van de boshelling waren op één vergeten *Orchis fusca* na alle bloeistengels afgeplukt (bescherming of misdaad?) Op onze terugweg vonden wij een prachtige afgeplukte *O. militaris*-stengel in een aardappelveld langs de weg netjes rechtop in een molshoop geplant, een hard gezicht, maar toch een welkome buit voor een florist, die zich met bloedend hart aan het „plukverbod" heeft gehouden. Verderop in een open plek in het bos een prachtige vegetatie van *Orchis militaris, fusca* en hun bastaard. Ook *Ophrys muscifera, Neottia* en *Cephalanthera pallens* werden nog mooi in bloei gevonden. *Gymnadenia*, die hier vroeger ook veel stond, is blijkbaar verdwenen, evenals *Cephalanthera ensifolia*. Intussen was ook deze laatste tocht weer zo heerlijk en de Orchideeën-weelde zo typisch Zuidlimburgs als van ouds, dat wij herhaaldelijk betreurden dat JANSEN en DE JONGH deze tocht niet meer mee konden maken, om tijdig huistoe te kunnen reizen. In Valkenburg nam ik afscheid van het gezelschap. SLOFF zou nog een dag in Meersen blijven, de overigen gingen door naar Maastricht en N. Nederland, zoals DE WEVER dat placht uit te drukken. Ik vertoefde nog twee dagen bij mijn vriend in Hulsberg. Op de lijstjes T6. **64**. 24, V6. **12**. 32, 41 en 42, die ik toen nog invulde, kwamen voor: *Atriplex hortense, Carex disticha, echinata* en *vulgaris, Chrysanthemum segetum, Galium palustre, Gnaphalium uliginosum, Holcus mollis, Mentha nemorosa, Nuphar, Raphanus sativus, Spergula Morisonii, Typha latifolia* en *Vicia tetrasperma*, een 14-tal dus, die wij blijkens de verzamellijst nog niet hadden waargenomen en die met de 523 van die lijst het aantal genoteerde soorten op 537 brachten.

Dordrecht, Juni 1948. Dr Ir A. W. KLOOS JR.

VERSLAG over het jaar 1948 van de Sub-Commissie voor het Zuiderzee-onderzoek.

In 1948 werd door de heer en mevrouw A. VAN DER WERFF en mejuffrouw A. P. C. DE VOS een excursie gemaakt rond het IJselmeer, waarbij vooral de wierenflora bekeken werd. BAKKER zette carteringswerkzaamheden in de Noord-Oostpolder voort. Het kustdeel Amsterdam-Diemen werd door PIET enige malen bezocht.

Het Correspondentieblaadje verscheen voor het eerst sedert twee jaar, waarmee deel VII werd begonnen. Behalve de laatste excursieverslagen werden hierin nog een tweetal bijdragen opgenomen.

Op de jaarvergadering in December 1948 werd voorgesteld in 1949 een excursie te houden langs het kustdeel Harderwijk-Nijkerk. De heer VAN DER WERFF verzocht het alcoholherbarium van de Zuiderzee-Commissie te doen opbergen in het Rijksherbarium te Leiden.

De wenselijkheid werd naar voren gebracht het onderzoek naar de wierenflora voort te zetten, en hierbij tevens de zuurgraad van het milieu te bepalen. Ook werd onderzoek naar de doorbraakkolken in de Wieringermeer bepleit.

De vergadering was van oordeel het Zuiderzee-onderzoek voort te zetten en nog niet de opheffing van de Sub-Commissie voor te stellen.

De Secretaris,
H. W. E. CROOCKEWIT.

VERSLAG van de Commissie voor de Biosociologie en het Veenonderzoek van Nederland over het jaar 1948.

In de samenstelling van de Commissie ontstond een wijziging door het aftreden van de leden Ir W. G. VAN DER KLOOT, Dr D. M. DE VRIES en Dr E. C. WASSINK, die vervangen werden door Ir P. R. DEN DULK, H. T. WATERBOLK en Dr F. P. JONKER, waarvan de laatste zich belastte met het secretariaat.

De Commissie organiseerde twee bijeenkomsten, de 21e en 22e Nederlandse Dag voor Biosociologie en Palaeobotanie, resp. op Zondag 25 April en Zondag 21 November, beide in de collegezaal van het Botanisch Laboratorium te Utrecht. De eerste van deze sociologendagen was geheel gewijd aan het onderwerp: „Bewegingen van Bodem en Zeeniveau in Nederland tijdens het Holoceen.” Door het speciale onderwerp was het aantal leden dat deze dag bijwoonde geringer dan gewoonlijk, nl. 29, en het aantal introducé’s groter, nl. 23. De eerste spreker was Dr F. P. JONKER (Utrecht) die een botanische inleiding gaf tot het onderwerp met een voordracht over „Het Botanisch Onderzoek naar het optreden van Transgressies en Regressies”. Vervolgens sprak Prof. Dr J. H. F. UMBGROVE uit Delft over de „Geologische Aspecten van Zeeniveau- en Bodembewegingen”, waarna van zoölogische kant het probleem benaderd werd door P. A. FLORSCHÜTZ (Utrecht), die „De mariene Mollusken uit de Holocene Afzettingen te Velzen” besprak. Hierna werd gepauzeerd en een gezamenlijke lunch gebruikt in het Universiteitshuis. In de middagvergadering besprak Ir T. K. HUIZINGA (Delft) de „Inklinking van de Grond” in verband met het onderwerp van deze dag, waarna de laatste spreker, Ir W. C. VISSER (Utrecht) sprak over het „Bodemkundig aspect van de Zeespiegelvariaties”. De op de agenda voorkomende samenvatting en bespreking van overeenkomsten en verschil van inzichten en resultaten, door Dr Mr F. FLORSCHÜTZ, moest wegens tijdgebrek achterwege blijven.

De 22e Sociologendag werd bezocht door 46 leden en 10 introducé’s. Achtereenvolgens spraken D. BAKKER (Kampen) over „De

Vegetatie van de toekomstige Zuid-Sloepolder", Dr M. J. ADRIANI (Alkmaar) over „Vergelijkend Waterbalansonderzoek" en Dr Ir E. MEYER DREES (Zutfen) over „Bosassociaties op Timor". Na de middagpauze, waarin wederom in het Universiteitshuis geluncht werd, spraken Ir J. BENNEMA (Loenen) over „Enkele voorlopige resultaten der Veenkartering in Zuid- en Noord-Holland", W. VAN ZEIST (Utrecht) over „Veenonderzoek van het Prinsenhof (Friesland)", W. MEYER (Amsterdam) over „Enkele Vegetatietypen in het Hollands-Utrechtse Veengebied" en J. J. BARKMAN (Leiden) over „Duinvegetaties van Noord-Schotland".

Ook dit jaar organiseerde de Commissie op Zaterdag 29 Mei een excursie naar de omgeving van Zeyen (Dr.) ter gelegenheid van de zomervergadering van de K.N.B.V. te Groningen; deze excursie werd voorbereid en geleid door ons commissielid H. T. WATERBOLK. De ongeveer 25 deelnemers vertrokken omstreeks 12.30 uur uit Assen per bus naar Zeyen. In het „Huis ter Jacht", waar de meegenomen boterhammen genuttigd werden, heette, bij ontstentenis van de voorzitter, de secretaris allen hartelijk welkom. Eerst werd bezocht het Bolleveen, een diep veentje aan de rand van de Zeyerstrubben. Cultuurresten uit de 4e eeuw na Chr. aan de basis van het jonge mosveen vormden het object van een opgraving, die door enige tegenslag met de pompinstallatie niet zo ver gevorderd was als wel gehoopt was. Men was hier de gast van de Rijksdienst voor het Oudheidkundig Bodemonderzoek (Hoofd Prof. Dr A. E. VAN GIFFEN). De hier verkregen gegevens omtrent de ouderdom van de z.g. grenshorizon van Weber werden uitvoerig besproken. Vervolgens werden de Zeyerstrubben bezocht, een rond de es van Zeyen gelegen bosgebied, bekend als groeiplaats van *Trientalis*, *Cornus suecica* en *Genista tinctoria*. Er werd gewezen op het voorkomen van verschillende subassociaties van het *Querceto-Betuletum*, nl. *typicum*, *violeteosum-Rivinianae* en *molinietosum*. Tenslotte werd – helaas in de regen – nog een bezoek gebracht aan het cultuurreservaat „het Noordse Veld", waar een hunebed, enkele tumuli en een z.g. heidense legerplaats – in werkelijkheid oud akkerland uit de tijd der urnenvelden – bezichtigd werden. Daarna werd de terugreis per bus naar Assen aanvaard, vanwaar de meeste deelnemers per trein naar Groningen vertrokken. De excursie was zo geregeld, dat men tijdig de avondvergadering kon bezoeken.

De Secretaris,
Dr F. P. JONKER.

Utrecht, 21 December 1948.

VERSLAG van de een en twintigste Nederlandse Dag voor Biosociologie en Palaeobotanie, gehouden op Zondag 25 April 1948 in de Collegezaal van het Botanisch Laboratorium te Utrecht.

Om half elf des ochtends werd deze vergadering, die tot onderwerp had: Bewegingen van Bodem en Zeeniveau in Nederland tijdens het Holoceen, geopend met een woord van welkom door de voorzitter, Dr A. SCHEYGROND.

De eerste spreker was Dr F. P. JONKER (Utrecht), die het onderwerp inleidde met een voordracht over:

Het Botanisch Onderzoek naar het optreden van Transgressies en Regressies.

In het Oud-Holoceen, voordat de tegenwoordige Noordzee ons land bereikt had, vormde zich een uitgestrekt veenlandschap, dat het tegenwoordige West-Nederland en het gebied van de Noordzee bedekte; fossiel staat het thans bekend als veen op grotere diepte. Aan de veengroei kwam een eind doordat de Noordzee ons land bereikte en op het veen mariene lagen afzette. De afzetting van het veen op grotere diepte is begonnen met veenvorming in een zoetwatermeer, dat langzamerhand dichtveende tijdens het boreaal en de eerste helft van het atlanticum. In de tweede helft van het atlanticum ontstond de verbinding met de Noordzee, de dichtgeveende baai werd overspoeld met zeewater dat wadafzettingen, oude duinen, de oude blauwe zeeklei etc. vormde. Dit hele proces werd aanvankelijk door TESCH opgevat als een gevolg van een voortdurende stijging van de zeespiegel, dus een ononderbroken transgressie sinds het Würmglaciaal. De eerste botanische aanwijzing dat deze transgressie wel eens onderbroken moet zijn geweest, vinden we in de hoogvenen van Oost-Nederland, waar het oude mosveen en het jonge mosveen gescheiden zijn door de grenslaag van WEBER, ontstaan in de subboreale periode. Deze grenslaag moet gevormd zijn, blijkens de botanische samenstelling, door een verlaging van de relatieve zeespiegelstand en de daarmee samenhangende wijziging in de edaphische omstandigheden. Deze aanwijzingen werden versterkt door het botanisch onderzoek van de West-Nederlandse bodem, waar de oude blauwe zeeklei en de jonge zeeklei dikwijls gescheiden zijn door een laagje veen, het oppervlakteveen, dat ook van subboreale ouderdom is. In die tijd verdween dus de zeeïnvloed en stond de flora onder invloed van het zoete grondwater. Tijdens de regressie in de subboreale periode verdween dus in het Westen de zeeïnvloed, waardoor veenvorming kon optreden, terwijl in het Oosten het grondwater zo sterk daalde, dat de veenvorming vertraagd werd. In het Westen bedekt de jonge zeeklei het oppervlakteveen, in het Oosten bedekt het jonge mosveen de grenslaag. D.w.z. er trad opnieuw een transgressie op. Een bouwput, gegraven voor de aanleg van een tunnel onder het Noordzeekanaal bij Velzen, bood een gelegenheid het Holoceen van West-Nederland te onderzoeken. Het laagterras bleek voltooid te zijn toen het boreaal ten einde liep. De bovenste 10 cm van het zand bestaan uit donker gekleurde bosgrond van een elzenbos. De wortels van deze elzen zijn tot 3 m het zand ingedrongen. Dit is een aanwijzing dat het grondwater, na de oppervlakte van het laagterras zo vochtig gemaakt te hebben dat er een elzenbos kon groeien, weer enige meters gedaald moet zijn. Een regressie dus tijdens het boreaal. Daarna steeg het grondwater opnieuw, inundeerde het laagterras zodat er een zoetwatermeer ontstond, waarin zich het veen op grotere diepte vormde.

MULLER en VAN RAADSHOVEN vonden in de N.O.-Polder deze boreale regressie niet, wel een onderbreking van de transgressie, resp. een kleine regressie tijdens het atlanticum, en wel in het middenatlanticum, dezelfde tijd dat het oude duinlandschap gevormd werd. Bij Velzen bevond zich in de kleilaag een duidelijke humusband, die als aanwijzing voor een plaats gehad hebbende midden-atlantische regressie opgevat kan worden.

In Nederland kennen we dus thans drie regressies: een boreale, een midden-atlantische en een subboreale. Deze drie regressies werden in N.W. Duitsland ook gevonden door SCHUETTE. In Engeland werd hetzelfde bestudeerd door GODWIN, die geen boreale regressie vond, wel een middenatlantische stagnatie en een subboreale regressie. Bovendien ontdekte hij aanwijzingen voor een regressie in historische tijd. Deze laatste was bij Velzen niet te constateren, maar misschien geeft het uitsterven van *Sphagnum imbricatum* in onze oostelijke venen een aanwijzing in die richting.

De opvattingen van SCHUETTE, die van GODWIN, en de uitkomsten van het onderzoek in Nederland werden graphisch voorgesteld. Uit de curve van Velzen kan zowel de stijging van de zeespiegel bij benadering berekend worden als 19 cm per eeuw als de oorspronkelijke dikte van het veen op grotere diepte, voor de samenpersing, worden berekend als 570 cm.

Hierna sprak Prof. Dr J. H. F. UMBGROVE (Delft), die de geologische aspecten van de zeeniveau- en bodembewegingen besprak in een voordracht, getiteld:

Bewegingen van Bodem en Zeeniveau in ons kustgebied gedurende de laatste 4000 jaren.

Het z.g. oude duinlandschap in onze westelijke provincies is gevormd tijdens de post-glaciale rijzing van het zeeniveau, de z.g. atlantische transgressie. Materiaal aangevoerd eensdeels uit het Noorden door de ijsmassa's, anderdeels door de grote rivieren, werd door de opkomende zee opgestuwd tot parallele zandruggen, tot een lido- of zandruggen-kust met er achter afzetting van de oude zeeklei. Op die zeeklei accumuleerde veen. Om deze verandering van zee naar landoppervlak in onze westelijke provincies te verklaren is het noodzakelijk te veronderstellen, dat de zee zich terugtrok uit dit gebied. Dit zou het gevolg kunnen zijn van opheffing van de bodem, daling van het zeeniveau of van een combinatie van beide.

Er is echter een daling van het zeeniveau in die z.g. subboreale tijd als een over de gehele wereld waargenomen verschijnsel bekend. Bovendien weten wij dat het zeeniveau sindsdien niet teruggekeerd is tot de hoogte waarop het vóórdien stond, doch thans ongeveer 6 m lager staat.

Dit algemeen bekende verschijnsel is voor het ontcijferen van de geschiedenis van ons kustgebied van groot belang. Ons land is gelegen in een bekkenvormige inzinking in de aardkorst. Deze indeuking begon te ontstaan ongeveer 200 millioen jaren geleden en de deuk werd geleidelijk aan opgevuld met afbraakproducten van de omringende gebieden. De gemiddelde bodemdaling (en opvulling) bedroeg nog geen halve centimeter per eeuw. Doch in bepaalde tijden was de beweging aanmerkelijk sneller — zoals wij nog nader zullen zien is dat thans het geval — in andere tijden langzamer. Dank zij de wereldwijde daling van het zeeniveau ongeveer 4000 jaren geleden is het nu mogelijk te zeggen hoeveel de bodemdaling sinds die tijd bedragen heeft. Het is nl. duidelijk, dat na de subboreale verlaging van het zeeniveau — een over de gehele wereld opgetreden verschijnsel — op een gegeven moment — locaal voor ons kustgebied — de zee weer ten opzichte van het land moest gaan stijgen, omdat nl. de bodemdaling het bedrag van 6 meter had „ingehaald". Vanaf dat moment werd de zee automatisch diens bondgenoot tegen ons. Deze voor ons kustgebied zo belangwekkende ommekeer vond plaats in de negende eeuw van onze jaartelling. Vanaf dat moment diende men zich intensief te gaan bemoeien met verdediging van de kust (inpoldering, bedijking, enz.). Bij deze relatieve stijging van het zeeniveau werd het kustgebied sterk aangetast. Uit het afbraakmateriaal van de oude zandruggen plus materiaal vrijgekomen door hervorming van het onderzeese kustprofiel ontstond onze duinreeks.

In de term bodemdaling zijn waarschijnlijk drie verschillende factoren verdisconteerd, nl. (1) compactie der sedimenten, ook

„klink” genoemd, (2) daling van de periphere gordel der laatste ijskap, (3) daling van de bodem van het bekken.

De totale bodemdaling heeft ongeveer 20 cm per eeuw bedragen, gemiddeld over de laatste 4000 jaren. Bovendien heeft er weer een recente stijging van het zeeniveau plaats gevonden van ongeveer 12 cm per eeuw. Deze is afgeleid uit een critische bewerking van een zeventigtal peilschalen over de gehele wereld. Ze houdt nauw verband met een algemeen terugtrekken van gletschers en ijskappen sinds ongeveer een eeuw, speciaal sedert het begin van de twintigste eeuw. Beweging van bodem en zeeniveau bij elkaar opgeteld zou dus ongeveer 30 cm saeculair geven voor de laatste eeuw. Dit bedrag klopt met het bedrag door sommigen afgeleid uit peilschaalwaarnemingen langs onze kust. (Zie voor een uitvoerige publicatie over het voorgaande: Proceed. Kon. Acad. v. Wetensch. Amsterdam, Vol. 50, afl. 3, 1947, p. 227-236).

De volgende spreker was de heer P. A. Florschütz (Utrecht); hij sprak over:

De mariene Mollusken in de Holocene afzettingen te Velzen.

Door enkele Utrechtse geologen werd geruime tijd geleden een aantal molluskenmonsters verzameld in de tunnelput te Velzen. Van de vele soorten worden hier slechts die besproken, die ons iets zeggen over het milieu waarin zij leefden.

In het veen op grotere diepte, dat te Velzen op 16,50—16,75 —NAP ligt, werden een aantal brakwatermollusken aangetroffen, nl. *Littorina saxatilis*, *Hydrobia stagnalis* en *Cardium edule* var. *paludosa* (een scheve, zeer dunschalige vorm). Uit het feit, dat van deze laatste Lamellibranchiaat enkele doubletten gevonden werden, mag men afleiden (met vrij grote zekerheid) dat de dieren terplaatse leefden. Deze fauna stemt vrijwel overeen met de molluskenfauna van de z.g. inlagen op Schouwen, waar men thans ook nog deze brakwaterdieren levend vinden kan. Ook de botanische vondsten van F. Florschütz in het veen op grotere diepte wijzen op een brakwaterlagune. Dat in deze veronderstelde lagune af en toe zeewater binnenstroomde kan men zien aan één van de monsters uit het veen. Daarin komen nl. verscheidene exemplaren van een zoutwatervorm van *Cardium edule* en verder *Spisula subtruncata* en *Macoma balthica* (beide ook dieren van zout water) voor. Deze schelpen kunnen bij een dergelijke instroming vanuit zee zijn ingespoeld.

Ondertussen steeg de zee voortdurend en overspoelde steeds veelvuldiger het veen. Het milieu werd zouter en op 16,10 m —NAP werden dan ook slibhoudende afzettingen met mollusken uit een zouter milieu tussen de brakwaterschelpen aangetroffen, o.a. *Rissoa membranacea*, *Hydrobia ulvae*, *Mytilus edulis* en *Cardium edule*.

Nog hoger, op 15,50 m beneden NAP, vinden wij de brakwatervorm van *Cardium edule* in het geheel niet meer. Wel vinden we typische wadbewoners als *Littorina littorea*, *Rissoa membranacea* en *Mytilus edulis*. In nog hoger gelegen lagen komen daar nog vele exemplaren van *Scrobicularia plana* bij, zodat we dan dus van een echt wad kunnen spreken. Daartussen treft men verspreid fragmenten van bewoners uit diepere zeegedeelten aan: *Macoma balthica*, *Barnea candida* en *Angulus tenuis*.

Tot en met 9 m —NAP blijft het beeld vrijwel gelijk. Het volgende monster was helaas eerst op 7,50 m verzameld. De hierin gevonden mollusken hebben zeer kleine afmetingen. Het opmerkelijke is, dat in deze laag geen *Littorina* meer voorkomt, hetgeen ook bij de hogere lagen het geval is. In deze hogere lagen ziet men *Cardium edule* var. *paludosa* weer optreden en wel verscheidene doubletten met periostracum. Ter plaatse bevond zich toen zeer brak water met zeer weinig invloed van de zee.

Hoewel wij uit deze altijd nog zeer kleine hoeveelheid monsters geen verstrekkende conclusies kunnen trekken, verdient het toch aanbeveling aan de hand van deze gegevens te trachten ons een beeld te vormen van de bewegingen van de zee ter plaatse van Velzen.

Zoals boven beschreven wijst de fauna van het veen op grotere diepte op het bestaan van een lagune, zeer brak water dus van de zee gescheiden door een zandwal. Hierin waren echter wel gaten, waardoor de zee af en toe binnen stroomde. Door voortdurende relatieve rijzing van de zeespiegel overstroomde het in de lagune afgezette veen. Het milieu werd steeds zouter en een wad ontstond. Dit vormde de oudholocene wadafzettingen.

Het ontbreken van *Littorina* in de lagen hoger dan 7,50 m —NAP kan een belangrijke aanwijzing zijn voor het verdere gedrag van de zee. *Littorina*-soorten zijn immers uitgesproken getijde-dieren. Zonder getijdenbeweging en dus periodieke droogte kunnen deze dieren niet leven. Ter plaatse van Velzen was dus blijkbaar geen getijdenbeweging meer merkbaar. Dit opent twee mogelijkheden:

1. De zee stond zo hoog, dat de laagwaterlijn ten oosten van Velzen lag.
2. De invloed van de zee was zodanig verminderd door een strandwal of duinenrij, dat in de brakke plas (getuige het voorkomen van *Cardium edule* var. *paludosa*) geen getijdenbeweging meer merkbaar was.

De eerste verklaring is vrijwel uitgesloten. In deze tijd werden de oude duinen gevormd. Deze duinenrij ontstond op een bestaande strandwal, doordat deze door een regressie van de zee droogliep. Men kan zich niet voorstellen, dat bij een zeestand met de laagwaterlijn ten oosten van Velzen een duinenrij ten westen van Velzen kan ontstaan.

We moeten dus de tweede verklaring als de waarschijnlijkste beschouwen. Deze is ook meer in overeenstemming met de voorstelling van Tesch e.a., dat de oude duinen een binnenmeer afsloten, dat langzaam verzoette en waarin af en toe enig zout water binnendrong. In dit binnenmeer werd de oude blauwe zeeklei afgezet. De grens van deze afzetting en de oud-holocene wadafzettingen ligt bij Velzen tussen 6 en 8 m —NAP.

Wanneer het vermoeden door voortgezet onderzoek van holocene mariene afzettingen in het westen van ons land geverifieerd kan worden en *Littorina* inderdaad in de hogere lagen ontbreekt, dan kan een palaeontologisch onderscheid gemaakt worden tussen de oud-holocene wadafzettingen en de oude blauwe zeeklei. Uiteraard zal bij langzaam terugtrekken van de zee deze scheiding niet scherp zijn.

Na de middagpauze sprak eerst Ir T. K. Huizinga (Delft) over:

Inklinking van de Grond.

In geschriften over de bodemdaling van Nederland wordt soms ook de „klink” of inklinking van de grond als medeoorzaak van dit verschijnsel vermeld. Deze klink vindt zijn oorzaak eensdeels in chemische omzetting, verwering of uitloging van de bovengrond, een verschijnsel, waaraan de landbouwkundigen veel studie wijden, anderzijds in een samendrukking onder uitpersing van poriënwater, welk verschijnsel veel dieper zijn invloed doet gelden. De grootte van de klink door samendrukking bedraagt vele malen die door chemische invloeden en wij willen daarom hierop wat nader ingaan.

De grond is een samenstel van korrels, water en lucht. Ieder van deze delen heeft zijn eigen spanning. In ons laaggelegen land en zeker voor de diepere lagen hebben wij meestal met luchtvrije grond te maken, dus met 2-fazige grond van korrels en water. Het is dan duidelijk dat de grondspanning σ_g op een bepaald vlak bestaat uit de korrelspanning σ_k plus de waterspanning σ_{w_1}, dus $\sigma_g = \sigma_k + \sigma_w$.

Wanneer wij een stukje van een dergelijke grond in een samendrukkingsring belasten, dan zien wij dat er een zetting optreedt waarvan de snelheid met de tijd afneemt (tijd-zakkingskromme). Bij een hogere belasting herhaalt zich dit verschijnsel. Wanneer wij nu de zettingen, tengevolge van die verschillende belastingen bereikt na bepaalde tijden, uitzetten tegenover de logarithme van de belasting, dan ontstaat een rechte lijn (lastzakkingskromme), waarvan de formule luidt:

$$z = \frac{h}{C} \lg \frac{p_1 + \Delta p}{p_1}.$$

Hieruit volgt, dat de zetting z groter wordt bij toenemende laagdikte h, bij grondsoorten met een geringere samendrukkingsconstante C, bij grotere belastingsverhogingen Δp en bij lagere korrelspanningen in het terrein p_1.

De samendrukkings-constante C, bepaald uit proefnemingen op ongeroerde grondmonsters, blijkt voor veen te bedragen 3-5, voor klei 10-20, voor leem 20-50, voor zand 50-300. Veen is dus zeer sterk samendrukbaar, zand over het algemeen zeer weinig.

Wanneer we ons afvragen hoe lang het duurt voordat deze zetting wordt bereikt, dan dient men te bedenken dat de zetting alleen veroorzaakt wordt door een uitstroming van het poriënwater, dat dus de stromingswetten van water in grond op deze samendrukking van toepassing zijn. Beschouwen wij nu 2 grondlagen, waarvan de ene n-× zo dik is als de andere, dan moet, omdat de samendrukking evenredig is met de laagdikte h, uit de dikke laag n-× zoveel water worden uitgeperst. Doch ook is de gemiddelde af te leggen afstand van dit water n-× zo groot, zodat de tijdsduur n^2-× zo groot is. In het laboratorium wordt de eindzakking voor 2 cm dikke monsters practisch bereikt voor zand na 5 minuten, voor klei na 30 dagen, voor veen na 7 dagen. Kan de afvloeiing van een 10 m dikke grondlaag in het terrein op dezelfde wijze geschieden als in het samendrukkingsapparaat, dan worden deze tijden voor het bereiken van dezelfde procentale samendrukking voor zand $2^1/_2$ jaar, voor klei ruim 20.000 jaar, voor veen 4800 jaar.

De theoretische afleiding van deze samendrukkings-theorie van VON TERZAGHI veronderstelt, dat de grond homogeen is wat zijn doorlatendheid betreft. Doch wanneer wij ons b.v. denken dat zij opgebouwd zou zijn uit lange ruime poriënkanalen, waarlangs moeilijk doorlatende korrelgroepen of bij aanwezigheid van geadsorbeerd water met een geheel andere viscositeit, dan zou de tijd, nodig voor een waterdeeltje om door het lange poriënkanaal af te stromen, in het niet zinken tegenover die, nodig om vanuit de korrelgroep of van het geadsorbeerde water naar dit kanaal te geraken.

Het zettingsverloop van dikke en dunne lagen zou dan vrijwel gelijk zijn. Men begrijpt, dat in het natuurlijke terrein veelal overgangen tussen deze twee uiterste gevallen zullen optreden.

Ook uit zettingsmetingen aan bestaande bouwwerken bleek, dat er vrijwel steeds een doorgaande en grotere zetting (seculaire zetting) optrad na een zekere beginperiode waarin de wet van VON TERZAGHI was gevolgd. Daarom zette prof. BUISMAN de tijdzakkingskromme op half logarithmische schaal uit en verkreeg hij voor allerlei zettingswaarnemingen een rechte lijn. Het bleek, dat bij proeven in het laboratorium deze lijn zelfs voor klei practisch na 1 dag, voor veen na 5 of 10 minuten ontstond. De samendrukking na een bepaalde tijd kan dan worden voorgesteld door $z = hp\,(a_p + a_s \log t)$ waarbij a_p de zetting na 1 dag bij een belasting van 1 kg/cm^2 en a_s die na vertienvoudiging van de tijd voorstelt. Voor onze Nederlandse gronden werden voor a_p en a_s de volgende waarden gevonden.

	a_p	a_s
veen	50	10
klei	15	3
leem	10	1

In verband met het vraagstuk dat ons vandaag bezig houdt, wil ik thans van deze theorieën die ik zeer summier heb moeten behandelen afstappen om U thans enige voorbeelden van zettingen te geven.

Voorbeeld 1.

Tijdens de uitvoering van het nieuwe sluizencomplex te Vreeswijk bleek, dat het maaiveld in de omgeving daalde, tengevolge van de voor de bouw toegepaste bronbemaling, waardoor de waterspanning in het onder het veen liggende zand daalde en nu het poriënwater uit het veen naar dit zand afstroomde. De spanning van het water verminderde dus, het gewicht van de grond bleef gelijk en dus nam de korrelspanning toe, met als gevolg een samendrukking. Bruggetjes die in het dalende terrein op palen waren gefundeerd, konden niet meer met wagens gepasseerd worden, omdat er als het ware een stoepje was ontstaan. Het terrein en enige markante punten zijn door de Rijkswaterstaat waargenomen en in tekening gebracht, waarbij zettingen van meerdere decimeters in enkele maanden tijds werden waargenomen.

Aan de hand van monsteronderzoek werd door het laboratorium achteraf een berekening uitgevoerd in verband met andere bemalingsobjecten en om het inzicht in deze verschijnselen te verduidelijken.

TERZAGHI was gevolgd. Daarom zette prof. Buisman de tijdzakkings-

Voorbeeld 2.

Bij de fabriek van Van Nelle in Rotterdam zal een groot terrein – de Spangenpolder – worden opgehoogd ten behoeve van nieuw te bouwen industrieën. Aangezien hier zeer dikke samendrukbare lagen aanwezig zijn werd ons gevraagd een onderzoek naar de te verwachten zettingen uit te voeren.

Wij hebben ter contrôle een berekening opgezet voor een terrein direct naast de fabriek van Van Nelle en deze berekening getoetst aan de gemeten zettingen van het terrein. Uit deze twee voorbeelden ziet U, dat door monsteronderzoek en berekening met vrij grote mate van nauwkeurigheid de te verwachten zettingen zijn te berekenen.

Voorbeeld 3.

De toekomstige hoogte van de N.O.-polder tengevolge van klink was voor de dienst van de Zuiderzeewerken van groot belang voor het vaststellen van de diepteligging van de uitwateringsgemalen. Bij deze drooglegging worden in de bovenlagen de korrelspanningen zeer verhoogd, omdat de grondwaterspiegel onder het maaiveld komt en de korrels dus geen opwaartse druk meer ondervinden. In de diepere lagen zal echter een opwaartse waterstroom ontstaan, waardoor de korreldruk afneemt. Wij hebben dus hier een toestand waar boven klink, beneden zwelling optreedt. De zwelling is in de regel ongeveer $^{1}/_{10}$ van de klink onder overigens gelijke omstandigheden. Uit monsteronderzoek en berekening werd door ons nu op vele plaatsen de te verwachten zetting berekend en een hoogtekaart van de toekomstige polder geconstrueerd. Vooral waar veel veen in de bodem aanwezig is zullen belangrijke zettingen optreden.

Voorbeeld 4.

Het is bekend dat onze oude polders lager gelegen zijn dan de jongere. Het Bodemkundig Instituut heeft de volume-gewichten van de bovengrond van de Dollardpolders vergeleken met de ouderdom. Dit verband werd grafisch weergegeven, terwijl onder de hoogteligging ten opzichte van NAP met de ouderdom is vergeleken. Men ziet dan dat deze metingen ook vrij aardig de logarithmische voorstellingswijze van Buisman volgen. Ook de hoogtematen van verschillende polders op het eiland Tholen t.o.v. de tijd van inpoldering op logarithmische schaal geven practisch een rechtlijnig verband. De helling van de lijn is hier flauwer dan die van de Dollardpolders, omdat de ondergrond meer zanderig is zoals uit de weergegeven boringen blijkt.

Voorbeeld 5.

Uit de ligging van de sloten is te zien dat de Binnendijkse Buitenveldse polder ten Z. van Amsterdam vroeger één geheel uitmaakte met het boezemland van Amstelland. In het boezemland ligt de waterspiegel ongeveer 10 cm beneden het maaiveld. In de polders is deze afstand in verband met de steeds toenemende landbouweisen thans ± 60 cm geworden, waardoor een zetting van ongeveer een meter is ontstaan in de tijd van 4 eeuwen. Wij verwachten nog een zetting van 30 cm in de volgende 200 jaar. In de westelijke provincies en o.a. ook in de polder de Koekoek, onderdeel van de polder Mastenbroek, kan men deze verschillen in hoogteligging waarnemen.

Het karakteristieke beeld van het Westen van ons land is op deze wijze eenvoudig te verklaren. De bewoners van deze gebieden is dit verschijnsel wel bekend, de boeren weten zeer goed dat ze door verlaging van het polderpeil ook hun land naar beneden halen. Dit gaat vanzelfsprekend het snelst in de veengebieden en des te langzamer hoe meer klei of zand in de ondergrond aanwezig is. Zodoende is thans uit de hoogteligging van het land een globaal oordeel over de grondgesteldheid te verkrijgen. In de polder Zegveld kent men namelijk de zgn. Lage en Hoge Broek. Het gemaal staat natuurlijk in de Lage Broek, maar thans is de toestand zo, dat de Lage Broek hoog ligt ten opzichte van de Hoge Broek. Dit laatste bevat veel klei in de grond, in het eerste wordt zuiver veen aangetroffen.

Wanneer wij nu met de samendrukkingsconstanten en de volume-gewichten van de grond, zoals wij die in het laboratorium hebben leren kennen, de zettingen berekenen, dan vinden wij dezelfde orde van grootte als ik U in deze voorbeelden heb vermeld. Dit was voor mij aanleiding om eens het profiel van Rotterdam op te bouwen aan de hand van de ouderdom van de lagen, zoals Dr Tesch die heeft vermeld. Deze opbouw is door prof. Faber in zijn boek op een meer inzicht gevende wijze weergegeven.

Uit deze voorbeelden blijkt, dat de klink van de grond door zuivere samendrukking vooral bij klei- en veengronden een factor is, die bij de bestudering van het vraagstuk van de bodemdaling van ons land niet mag worden vergeten. Teneinde over deze daling juist te worden ingelicht staan ons in hoofdzaak peilschaalwaarnemingen en waterpassingen over langdurige tijdstippen ten dienste. De peilschalen en vaste merkpunten dienen daarom op vaste, diep gelegen gronden gefundeerd te worden.

Ten slotte wil ik opmerken dat deze verschijnselen ook voor de geologen van eminent belang zijn, waarbij wij slechts behoeven te denken aan de samendrukking van het veen tot onze koollagen in het zuiden van het land.

De laatste spreker was Ir W. C. Visser (Utrecht); zijn voordracht was getiteld:

Bodemkundig Aspect van de Zeespiegelvariaties.

Het onderzoek van het bodemprofiel geeft de indruk, dat de variaties van de zeespiegel ten opzichte van het land hun oorzaak vinden enerzijds in de gelijkmatige daling van de bodem ten gevolge van zowel tectonische oorzaken als van klink, waarover een periodieke verandering van de zeespiegel gesupponeerd moet worden gedacht. Deze verschijnselen gaan ook in de laatste tientallen eeuwen nog regelmatig voort, zodat de verwachting kan worden uitgesproken, dat wij thans aan het begin van een nieuwe transgressie-periode staan. Deze opvattingen kunnen worden gedemonstreerd aan gegevens, die uit het rivierkleigebied werden ontleend. De verhogingen van de erosiebasis heeft aanleiding gegeven tot periodieke sedimentaties, waarbij de rivier de tendenz had te verzanden en verlegging van de rivier optrad.

Deze perioden werden afgewisseld door perioden van regressie, verlaging van de erosiebasis dus, waarbij de rivier zich wat dieper insneed en het regime veel conservatiever was.

Men kan zich het rivierlandschap voorstellen te zijn opgebouwd uit lagen, welke door een tijdelijk rivierenstelsel werden afgezet, welke lagen boven elkaar liggen en telkens een apart systeem hebben gevolgd. De dikte van deze lagen varieert van 50 cm in het Oosten van ons land tot 1 m in het Westen. De afzetting van een dergelijke laag heeft vermoedelijk 5 tot 6 eeuwen geduurd en wordt gescheiden van een vorige of volgende periode van afzetting door een ongeveer even lange tijd van rust.

De onderscheiding van deze opeenvolgende afzettingssystemen kan op verschillende wijze geschieden.

De archaeologie kan oudere bodemoppervlakken aanwijzen en dateren. Ook het pollenonderzoek kan aantonen, hoe perioden van relatief lage waterstanden wisselen met perioden van relatief drassige omstandigheden. Men kan uit een overkomde rivierloop de stroombaan uit voorhistorische tijden reconstrueren en aantonen hoe daar lagen boven elkander optreden.

Ook de variaties in het slibgehalte in het profiel zijn aanwijzingen voor het optreden van stroombedverleggingen, waarbij zandige gronden wijzen op de nabijheid van de rivier, terwijl hoge slibgehalten het bewijs vormen van de afzetting van een komgrond, welke op grote afstand van de rivier verwacht moet worden. Men kan zich het gehele riviergebied als een maquette voorstellen, opgebouwd uit lagen van min of meer gelijke dikten of iets gewelfd oppervlak, hoog ter plaatse van de oeverwalafzettingen van de rivier, 1 tot 2 meter lager in de kom, waaronder men wederom dezelfde typen van lagen aantreft, die het rivierenstelsel in een ± 1000 jaar oudere periode weergeeft.

Een dergelijke laag geeft dan weer ongeveer hetzelfde beeld, doch de ligging van de rivier en de kom is aardrijkskundig gezien daar een andere.

In de grond treft men dus zandbanen aan, die op verschillend niveau zich door de grond kronkelen en elk op een eigen diepte lopen.

Wanneer men dit beeld kent, ontstaan mogelijkheden van datering van deze verschillende rivierenstelsels en kan men een voorspelling doen van cultuurtechnisch belangrijke kwesties bij het profiel, speciaal de mogelijkheid van drainage, kwel, stevigheid van slootranden, geschiktheid voor bepaalde cultuur enz.

Hiernaast kan de nauwkeurige kennis van het cyclisch verloop van transgressies en regressies een waardevolle grondslag zijn voor het verklaren van allerlei culturele verschijnselen op allerlei gebied. Er bestaan banden tussen het gedrag van de zeespiegel en het bouwen van terpen, het aanleggen van dijken, het optreden van volksverhuizing en het ontstaan van een arbeidsoverschot, dat tot grotere welvaart leidt.

De Palaeobotanie kan dientengevolge medehelpen aan het ontsluieren van vele vraagstukken uit het verleden en kan geëxtraponeerd inzicht geven over vermoedelijke toekomstige klimaatsveranderingen en gedragingen van de zeespiegel.

De hierna op de agenda vermelde samenvatting van de voorgaande voordrachten en bespreking van overeenkomst en verschil van inzichten en resultaten, door Mr Dr F. Florschütz (Velp-Gld.), kon wegens het vergevorderde uur niet doorgaan. De voorzitter sloot hierop deze goed bezochte vergadering.

VERSLAG van de twee en twintigste Nederlandse Dag voor Biosociologie en Palaeobotanie, gehouden op Zondag 21 November 1948 in de Collegezaal van het Botanisch Laboratorium van de Rijksuniversiteit te Utrecht.

Om half elf des ochtends werd deze 22e „Sociologendag” door de voorzitter, Dr A. Scheygrond, geopend met een woord van welkom tot de 46 leden en 10 introducé’s, die deze vergadering bijwoonden. Nadat hij de benoeming van ons commissielid Dr Mr F.

FLORSCHÜTZ tot bijzonder hoogleraar te Leiden en de verschijning van de eerste aflevering van het tijdschrift „Vegetatio" gememoreerd had, stelde hij aan de orde het opmaken van een voordracht aan de ledenvergadering ter voorziening in de vacature, ontstaan wegens het periodiek aftreden van Dr A. SCHEYGROND als lid en voorzitter van de Commissie voor de Biosociologie en het Veenonderzoek van Nederland.

Besloten werd Prof. Dr J. HEIMANS candidaat te stellen.

Daarna was het woord aan de eerste spreker, de heer D. BAKKER (Kampen), die sprak over:

De vegetatie van de toekomstige Zuid-Sloepolder.

Tussen Walcheren en Zuid-Beveland strekte zich oorspronkelijk een breed water uit, Vlakke genaamd, waarin schorren en platen lagen, doorsneden door geulen. Het Vlakke kreeg later de naam Sloe. Door vele inpolderingen, die reeds in de 16e en 17e eeuw een aanvang namen, werd het Sloe steeds smaller. In 1871 werd de dam tussen Zuid-Beveland en Walcheren gebouwd, waardoor het Noord- en Zuid-Sloe ontstonden. Vanaf dit tijdstip ging de aanslibbing in dit gebied zeer snel. In 1925 plantte men in het Sloe *Spartina Townsendii* H. et J. Groves uit. De aanslibbing werd door deze plant sterk bevorderd.

Van het Zuid-Sloe wordt in 1949 het Noordelijk gedeelte, groot 458 ha, ingepolderd. In tegenstelling met het zandige Noord-Sloe bestaat de bovenste bodemlaag (gemiddeld 1 m) uit zware klei (± 45% afslibbare delen) met een koolzure kalkgehalte van 17 tot 22%, hetgeen zeer hoog is. De doorlatendheid van de grond is, met uitzondering van de schapendreven, goed. De aëratie van de bodem heeft, met uitzondering van de schapendreven en de laagste plekken, tot op grote diepte plaats (gemiddeld 80 cm).

Het gebied bestaat uit twee oude schorcomplexen, voor het grootste gedeelte omgeven door een jong, met *Spartina Townsendii* begroeid slik. Langs de oever van Zuid-Beveland loopt een diepe onbegroeide kreek, deze buigt op de hoogte van de oude veerdam naar binnen. In deze kreek monden vele kreken en kreekjes uit, die de oude schorren en het Spartina-gebied grillig doorsnijden.

De beide oude schorren zijn door een afgedamde en daarna dichtgeslibde kreek verbonden. De kreken en kreekjes worden omzoomd door oeverwallen, die merkwaardigerwijs uit even zware klei bestaan als de tussenliggende kommen. Bij de uitmonding van de kreken en kreekjes in de grote kreek vloeien de ruggen samen.

Het Spartina-gebied ligt iets lager (± 10 cm) dan de oude schorren, het slib is er veel slapper dan op het oude schor. De Spartina heeft bovendien lage gedeelten van de oude schorren ingenomen.

Het Zuid-Sloe is arm aan soorten hogere planten. Totaal vond ik 13 soorten, terwijl de nabijgelegen Kaloot 23 soorten opleverde. De gelijkmatige bodem, de geringe hoogteverschillen en het domineren van *Spartina Townsendii* kunnen voor dit geringe soortenaantal aansprakelijk gesteld worden.

De diepe kreken zijn niet begroeid door hogere planten, slechts een wiervilt bedekt plaatselijk de bodem.

Het *Salicornieto-Spartinetum* Br.-Bl. et de L. en eveneens de lagere gedeelten van het *Puccinellietum maritimae* Br.-Bl. et de L. zijn vrijwel geheel verdrongen door *Spartina Townsendii*. Geïsoleerd komen in sommige dichtgeslibde kreekjes nog resten van het *Salicornieto-Spartinetum* met *Salicornia herbacea* L. ssp. *stricta* G. Meij. voor. *Spartina stricta* Roth is geheel verdwenen.

In de *Spartina Townsendii*-begroeiing komen verder nog *Suaeda maritima* Dum., *Atriplex hastata* L. en *Aster Tripolium* L. voor. De drie laatstgenoemde soorten met *Puccinellia maritima* Parl. en *Obione portulacoides* Moq. krijgen de overhand op de jonge oeverwallen, terwijl *Spartina Townsendii* verdwijnt.

Op de laaggelegen schapendreven komt *Spartina Townsendii* niet voor. De vastgetrapte bodem is ongeschikt voor deze plant, die een slappe slikbodem verkiest. Op de schapendreven domineert *Salicornia herbacea*. Het is echter niet de ondersoort *stricta* G. Meij. van het *Salicornieto-Spartinetum*, maar een gedrongen vorm. In de zomer kan het zoutgehalte in de bovenste lagen van deze schapendreven sterk oplopen, daar ze alleen bij hoge vloeden onderlopen en de uitspoeling in deze ondoorlatende grond gering is.

Het *Puccinellietum maritimae* neemt een groot gedeelte van de lagere stukken van de oude schorren in. *Spartina Townsendii* dringt hierin nog steeds naar voren. Op geringe terreinverhogingen treft men hier facies van *Obione portulacoides* aan.

Op de oude oeverwallen domineert *Triticum litorale* Host. Alleen bij springvloeden lopen de oeverwallen nog onder. De zoutgehaltes wisselen er sterk en kunnen nog vrij hoog zijn. Men zou op deze oeverwallen het *Artemisietum maritimae* Br.-Bl. et de L. verwachten. *Artemisia maritima* L. komt maar sporadisch op het Zuid-Sloe voor, *Limonium vulgare* Mill. ontbreekt geheel, terwijl *Obione portulacoides* tot de kommen beperkt is. Vermoedelijk spelen de dichte vloedmerken die op deze oeverwallen afgezet worden hierbij een belangrijke rol. *Artemisia* en *Obione* kunnen een bedekking door deze dikke vloedmerken slecht verdragen. *Triticum litorale* herstelt zich spoedig weer van een bedekking door een vloedmerk. Soms krijgt men zelfs de indruk, dat de ontwikkeling van *Triticum* door de aanwezigheid van vloedmerken gestimuleerd wordt (veel N). Zijn de vloedmerken zeer dik dan ontwikkelt zich daar tijdelijk een begroeiing van de nitrophiele *Atriplex hastata* op.

Op de hoogste plaatsen treft men kleine weiden van *Festuca rubra* L. aan.

Als tweede spreker kreeg het woord Dr M. J. ADRIANI (Alkmaar) met een voordracht, getiteld:

Over vergelijkend Waterbalansonderzoek.

De plantensociologie (phytocoenologie) heeft verschillende facetten; de oecologie is daar één van. Door de samenhang tussen de plant en haar milieu als haar domein af te bakenen, tracht zij het samen-voorkomen van planten in de sociologische eenheden te verklaren. De oecologie alleen kan echter niet volledig tot dit doel geraken, daar steeds factoren van historische aard (b.v. vegetatiesuccessie, invloed van mens en dier) mede in het geding moeten worden betrokken.

De doelstelling van de oecologie is *finaal*; zij wil laten zien, op welke wijze en hoe verfijnd het levende organisme is ingepast in het milieu, waarin het voorkomt.

Het waterbalansprobleem is sinds SCHIMPER's dagen actueel geworden en gebleven. SCHIMPER's conceptie van xerophyten en van het physiologisch droog-zijn van moerasstandplaatsen en van bodems, die een hoge concentratie aan zouten bevatten, stimuleerde het transpiratieonderzoek, daar SCHIMPER suggereerde, dat hèt xerophytenkenmerk bij uitnemendheid een geringe transpiratie was. Moeilijkheden ontstaan bij vergelijkend transpiratie-onderzoek, daar men geen bevredigende grootheid kan vinden, waarop de transpiratie betrokken moet worden.

Deze wijze van onderzoek moest wel onbevredigend blijven, daar men de transpiratie niet los kan denken van het geheel van de waterbalans. Deze opvatting brengt met zich mede, dat vergelijkend transpiratie-onderzoek slechts dan op een quantitatieve basis kan plaats vinden, als men de transpiratie betrekken kan op een grootheid, waarin *alle* factoren verantwoord zijn, die te maken hebben met wateropname, watertoevoer en waterafgifte. Dit behoort uit de aard der zaak tot de zgn. vrome wensen. Daarom is het juister om bij vergelijkend waterbalans-onderzoek andere criteria te gebruiken, welke samengevat kunnen worden in de volgende vragen: welke variaties verdraagt het levende protoplasma in de osmotische waarden (hydratuur), en ook: hoe lang vermag de plant, ook bij groot waterverlies, haar stomata geopend te houden, dit laatste met het oog op de CO_2-assimilatie? Naar deze criteria worden drie typen van xerophyten besproken:

1. Planten, die een grote variabiliteit in haar osmotische waarde toelaten, en tevens haar stomata lang geopend houden. Vb.: vele steppeplanten, *Obione portulacoides*.
2. Planten, die een geringe variabiliteit vertonen, maar gedurende de gehele vegetatie-periode geregeld en continu transpireren. Bomen en struiken in het Middellandse Zee-gebied. Diepe doorworteling.
3. Planten met betrekkelijk geringe variabiliteit in haar osmotische waarde, en een zeer geringe transpiratie. Succulenten. Deze vertonen dan ook bijzondere dissimilatieverschijnselen.

De waterbalans van het halophyten wordt nog even aangeroerd, waarbij treft, dat op de standplaats van het *Salicornieto-Spartinetum* — vrijwel enig in zijn soort — halophyten bijeen staan, welke grondig van elkaar verschillen wat betreft het type van hun waterbalans.

Ten slotte wordt de gedachte naar voren gebracht, dat ook de oecologie bij de bioloog in sterke mate de notie kan versterken, dat ieder levend wezen een *gaaf geheel* is, ingepast als het is in zijn milieu.

Vervolgens sprak Dr Ir E. MEYER DREES (tijdelijk te Zutfen) over:

Bosassociaties op Timor.

Sterk wisselende oecologische omstandigheden doen de begroeiing op Timor zeer variëren. Het klimaat is aan de N.-kust uiterst droog, in het Z.O.-deel en in het gebergte (Moetis: 2400 m) vrij vochtig; de bodem variëert van zure kristallijnen schisten over basische andesiet en gabbro naar mergel en kalksteen, afgezien nog van alluviale zand- en klei-afzettingen. Daarbij komen nog de uitgesproken halophiele gronden langs de kust en enkele vlakten in het binnenland, die verdacht worden van een door de droogte veroorzaakt hoog gehalte aan zouten. Ook in het allerdroogste gebied is de climax nog bosachtig; in het Z.O. nadert het bos het tropische regenbos. Brand en veeweide hebben van het primaire bos echter bijna niets overgelaten: de begroeiing is overwegend steppe en savanne.

De verschillende typen primair bos blijken tot een schema samengesteld te kunnen worden dat hun volledige onafhankelijkheid van het moedergesteente bewijst. Daarentegen is het secundaire bos (dat is in de regel savanne of savannebos) in zijn samenstelling overwegend bepaald door de bodem. Daar deze savannen zich zonder speciale tussenstadia tot de climax herstellen, vindt men in deze overgangen indicaties voor bodem en klimaat verenigd. Hierin ligt de belangrijkste betekenis voor de praktijk van de bosbouw.

Naast restanten van het climax-bos treft men nog verschillende vormen van subclimax-bossen op hoog grondwater aan. Ook deze hebben hun secundaire parallellen als savannebos. Uit de aard der zaak zijn ze in hoge mate onafhankelijk van bodem en klimaat beide.

Bij het uitwerken van de associatie-tabellen (die geheel in de geest van de Frans-Zwitserse school werden opgezet) bleek, dat onder de houtachtige gewassen kensoorten slechts sporadisch aanwezig zijn zodra men grotere gebieden onderzoekt. Ook het opstellen van hogere eenheden stuit op moeilijkheden, daar men op verschillende eilanden verwante vicariërende associaties aantreft, zodat de plaatselijke groepering evengoed vervangen kan worden door een classificatie *over* de verschillende eilanden.

De conclusies luiden dan ook: *a.* dat men geen kensoorten mag postuleren, maar hun aan- of afwezigheid van het resultaat van het onderzoek moet laten afhangen; *b.* dat, wil men een multidimensionale classificatie ontgaan, men zich moet beperken tot geografisch goed begrensde gebieden (i.c. eilanden of eilanden-groepen).

Onder deze voorwaarden is plantensociologisch onderzoek volgens de methoden der Frans-Zwitserse school in de tropen even goed mogelijk als in gematigde gebieden. M.i. geldt dit ook voor het aequatoriale regenbos.

Hierna verkreeg Ir J. BENNEMA (Loenen a. d. Vecht) het woord voor het houden van zijn voordracht over

Enkele voorlopige resultaten der veengrondenkartering in West-Nederland.

In het kader der werkzaamheden van de Stichting voor Bodemkartering te Wageningen wordt een studie gemaakt van de veengronden in Utrecht, Zuid- en Noord-Holland. Het doel hiervan is een goede indeling van deze gronden te maken, waarbij enerzijds rekening wordt gehouden met de genese en anderzijds met de landbouwkundige eigenschappen van het veen.

Bij deze studie zijn vooral de bovenste lagen van het veenprofiel van belang, zodat in het onderstaande voornamelijk over deze lagen gesproken zal worden. De landbouwkundige eigenschappen zullen hier onbesproken blijven.

Op het ogenblik zijn er slechts schamele resten over van het oorspronkelijk veenoppervlak. Bij het ontstaan van de grote meren in Noord- en Zuid-Holland werden belangrijke delen van het veengebied opgeruimd. Later werden vooral in Zuid-Holland en Utrecht grote gebieden uitgeveend. Door de overgebleven veenribbels, die eertijds de grenzen tussen de verschillende verveningen vormden, mede in het onderzoek te betrekken, kan toch nog een vrij goed beeld van de oude toestand verkregen worden.

Op het veen in Westelijk Nederland ligt over grote oppervlakten een kleilaagje, dat in dikte en de aard sterk kan verschillen en dat slechts zelden geheel ontbreekt. Dit kleilaagje begint vaak als een kleiig-zeggeveen.

Wij zullen nu nagaan uit welke veentypen de bovenste meter van het veengebied, ontdaan van zijn kleilaagje, bestaat en hoe deze typen in horizontale zin ten opzichte van elkaar gelegen zijn. Er wordt hierbij uitgegaan van de vroegere toestand, van voor de grote verveningen.

Langs de Lek, de Waal, de Maas, de Oude Rijn, de Hollandse IJsel en de Vecht bevinden zich grote complexen bosveen. Ook langs de kleinere zijrivieren van de Oude Rijn, zoals de Mije, de Drecht, de Kromme Mijdrecht, de Amstel en de Angstel, bevindt zich dit veentype, doch hier zijn het slechts smalle stroken. In dit veen valt macroscopisch alleen het hout, liggend in een bruine, slibberige grondmassa op. Deze grondmassa bestaat uit sterk veraard, organisch materiaal, dat gemengd is met kleinere of grotere hoeveelheden rivierklei. Het hout is voor een groot deel afkomstig van de els, maar ook andere houtsoorten, zoals de wilg en de es, komen er regelmatig in voor. Plaatselijk vindt men bovendien vrij veel eiken. Wij hebben de indruk, dat deze in een bepaald niveau, dat zich op ongeveer 1 m onder het maaiveld bevindt, voorkomen. Het zijn soms oude bomen, die slechts langzaam gegroeid zijn.

De planten-gezelschappen, waaruit dit veen is ontstaan, zullen wel tot de *Alnetalia* gerekend moeten worden. Uit het regelmatig voorkomen van de es en soms van de eik blijkt echter ook, dat er een zekere verwantschap met het *Fraxino-Carpinion* aanwezig is.

Aan de riviermonden, waar de zee nog enige invloed heeft gehad, vinden we vooral rietveenprofielen. In dit veentype vallen, behalve de wortelstokken van het riet, ook de knollen van de zeebies op. In het gebied ten westen van Rotterdam treffen we dit veen over een vrij grote uitgestrektheid aan, evenals b.v. in het gebied van Muiden.

Ook buiten de riviermondgebieden wordt dit veentype soms gevonden. Een voorbeeld hiervan is het gebied ten westen van Assendelft. Dit wijst er hier op, dat de zee tegen het einde van de veengroei nog invloed in dit gebied heeft uitgeoefend.

In de meeste gevallen ligt het rietveen op de oude, blauwe zeeklei, soms echter ligt het boven op mesotroof of oligotroof veen. Dit laatste werd o.a. bij Monnikendam en ten zuiden van de IJpolders aangetroffen. Hier is dus blijkbaar het oorspronkelijke veen verdronken. Nu is het merkwaardig, dat er zich in een aantal gevallen een nieuw oligotroof veenlaagje op dit rietveen heeft gevormd. Op dit oligotrofe laagje ligt dan weer vaak het reeds eerder vermelde kleilaagje. Er is hier dus een afwisseling van verdrinken en weer droog komen van het betrokken gebied. Of dit te wijten is aan wijzigingen in de zeespiegelstand, of aan plaatselijke omstandigheden, is in het huidig stadium van onderzoek niet uit te maken.

Buiten de invloed der rivieren en van de zee gaat het eutrofe riet- en bosveen over in mesotroof en oligotroof veen. Zo grenst aan het bosveen vaak berken-zeggeveen, dat nog verder van de rivieren af meestal in oligotroof mosveen overgaat.

In de gebieden, die niet beïnvloed worden door rivier- of zeewater wordt dit laatste veentype echter niet overal aangetroffen. Zo vinden we aan de rand van de Utrechtse heuvelrij en achter de duinen ook een strook mesotroof veen, vaak bestaande uit een veensoort met veel bladmossen en met kleine zeggen. Ditzelfde veentype komt ook in vrij grote uitgestrektheid voor ten noorden van Edam. Het is dezelfde veensoort, die we ook overal onder het oligotrofe veen kunnen aantreffen. Dit veen is in de aangegeven gebieden dus blijkbaar doorgegroeid, zonder dat het tot belangrijke oligotrofe veengroei is gekomen. Achter de duinen en bij de Utrechtse heuvelrij is het kwelwater hiervan waarschijnlijk de oorzaak. De voornaamste plantengezelschappen, die dit veen vormden, behoren vooral tot de *Caricetalia fuscae.*

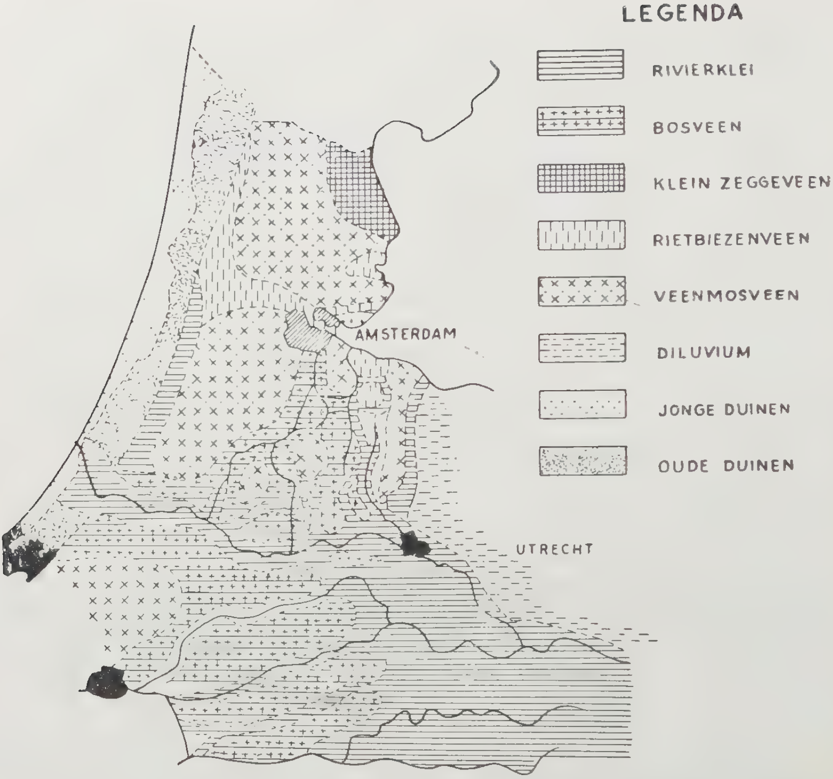
In het door ons beschouwde gebied vinden we, begrensd door meso- en eutroof veen, een drietal oligotrofe complexen. Hier bestaat de bovenste meter van het profiel meestal uit mosveen. Deze complexen zijn:

a. *Het Vechtplassengebied.* Dit gebied wordt in het westen begrensd door de brede bosveenstrook van de Vecht en zijn zijrivieren en in het oosten door een smalle strook mesotroof veen langs de Utrechtse heuvelrij. Het grootste deel van dit complex is thans verveend.

b. *Een gebied ten westen van Gouda,* in de hoek tussen de Hollandse IJsel en de Oude Rijn. Ook dit gebied is voor het grootste deel verveend.

c. *Een gebied benoorden de Oude Rijn.* Dit beslaat een groot deel van Zuid-Holland en een aanzienlijk deel van Noord-Holland. Hoewel in dit gebied ook veel veen vergraven en verslagen is, is er toch nog een belangrijk deel overgebleven.

Buiten Holland en Utrecht vinden we nog grote oligotrofe



veengebieden in Friesland-Overijsel en in West Brabant-Zeeland.

Het blijkt, dat men vroeger vooral de oligotrofe gebieden heeft verveend. De eutrofe gebieden, waarin vaak klei in het veen voorkomt, leenden zich hiertoe in het algemeen minder goed.

Het bovenste deel van het oligotrofe veenpakket wordt vaak gevormd door zogenaamd jong-mosveen, dat meestal als grofbladig veenmosveen (*cymbifolia*-veen) is ontwikkeld. Dit veen ligt dan op een type, dat oud mosveen genoemd kan worden. Het jong-mosveen is echter lang niet altijd aanwezig. Vaak vindt men bovenop een veentype, dat het meest op oud-mosveen gelijkt. Er is geen reden aan te nemen, dat de veengroei hier eerder tot stilstand is gekomen, of dat het jong-mosveen er afgeslagen is. Waarschijnlijk heeft het type jong-mosveen zich tegelijkertijd naast het type oud-mosveen ontwikkeld. Het laatste type bestaat in het algemeen uit vergaan veenmos en veel kleine, rode worteltjes, die waarschijnlijk van dopheide afkomstig zijn. Ook treffen we er wollegras en grove wortelstokken van de struikheide in aan. Slechts af en toe is de struikheide een belangrijke component in dit veen.

Aan de hand van enkele bodemkaartjes werd het een en ander verduidelijkt.

De volgende spreker was de heer W. VAN ZEIST (Utrecht); zijn voordracht was getiteld:

Veenonderzoek van het Princehof (*Friesland*).

Het Princehof vormt een restant van het eertijds uitgestrekte Friese veengebied. De dikte van het veen boven de fluvio-glaciale ondergrond wisselt sterk (50 cm tot ruim 3 m). In dit gebied ligt op het veen een kleilaagje dat naar het W. en N.W. sterk in dikte toeneemt. Eén diagram gaat tot het Praeboreaal, overwegend *Betula* met de eerste thermophiele bomen (*Corylus*, *Alnus*) en een hoog *Cyperaceae*-percentage. Op diverse plaatsen is in het zand onder het veen een oerbank aangetroffen, wat dus zou wijzen op een oorspronkelijke heidevegetatie. Hiervan is in de diagrammen niets te zien, de *Ericaceae*-percentages zijn steeds aanvankelijk zeer laag.

De veengroei is in het Boreaal gering geweest; de Berk zal althans plaatselijk, nog een belangrijke rol gespeeld hebben. Een *Corylus*-maximum is hier niet aangetroffen in het Boreaal, dit komt eerst in het vroeg Atlanticum.

In het Atlanticum was de veengroei sterk; men mag aannemen dat in deze tijd eerst de veenvorming in het gehele gebied begon. Vaak beginnend met een moerasbos, daarna een Zeggenveen, dat ten slotte overgaat in het oude-mosveen, dat naar boven toe zeer *Ericaceae*-rijk wordt. Pollenanalytisch vertoont het Atlanticum geen bijzondere dingen, *Alnus* blijft hoog (60 70%), het *Quercetum-mixtum* heeft in het vroeg Atlanticum een klein maximum, schommelt verder tussen de 10 en 25%. *Corylus* blijft ook goed vertegenwoordigd. *Picea* komt schaars voor. In het Atlantische veen werden twee smalle kleibandjes aangetroffen, waarin o.a. vrij veel stuifmeel van *Compositae*, *Gramineae*, *Chenopodiaceae* en *Caryophyllaceae* bleek te zitten. Dit wijst dus op een halophyten-begroeiing. De Atlantische overstromingen van de zee zullen in dit gebied ongeveer hun grens bereikt hebben, gezien de dunne kleilaag en de halophytenvegetatie. Dit resultaat komt goed overeen met dat in de N.O.-polder, waar MULLER en VAN RAADSHOVEN ook twee Atlantische transgressies onderscheiden.

Een grenshorizon was niet te zien. De overgang Subboreaal-Subatlanticum is te reconstrueren uit het plotselinge afnemen van de *Ericaceae*-curve en de opkomst van *Fagus*, die overigens in het Princehof nergens de 10% bereikt. Dit laatste is in overeenstemming met de hypothese van OVERBECK en SCHMITZ. De Sub-atlantische curven hebben een heel normaal verloop.

Het jonge mosveen is opgebouwd uit *Sphagna* van de *Cymbifolia*-groep, eerst *Sphagnum imbricatum*, later *Sphagnum palustre*. Door de Subatlantische transgressie kan het jonge-mosveen plaatselijk geheel weggeslagen zijn. In de klei boven het veen loopt *Pinus* plotseling op, wat echter wel niet zal wijzen op een uitbreiding van *Pinus*. De eerste menselijke invloed had plaats in het begin van de 12e en 13e eeuw, toen verveningen op vrij grote schaal plaats hadden.

De zesde spreker was de heer W. MEYER (Amsterdam) met een voordracht, getiteld:

Enkele problemen bij vegetatie-studie in West-Nederlandse venen.

De vegetaties van onze W.-Nederlandse plassen en moerassen, in zekere opzichten uniek in West-Europa, zijn zeer geschikt voor het uitvoeren van veldbiologische studiën. Een eerste eis bij dergelijk onderzoek lijkt ons een ruime, onbevooroordeelde visie.

Gedurende enkele seizoenen tijdens de oorlog en daarna werd in Zaanstreek, Waterland, Naardermeer en Vechtplassengebied vegetatie-kundig werk verricht. Bij het uitwerken van deze gegevens kwamen vooral problemen over systematische aanpak naar voren. Aan de hand van kijkjes in een drietal van genoemde terreinen werden deze problemen belicht. Door het doen van vele waarnemingen verkreeg men een beeld van de uiteenlopende successiereeksen in dergelijke gebieden. Achtereenvolgens werden nu de mogelijkheden om het materiaal op Noordse of Frans-Zwitserse methode te bewerken besproken. Principiëel werd de vraag gesteld of het vaststellen van associaties in deze vegetaties zin heeft. Zo niet, dan kan men volstaan met de af te grenzen stadia te paralleliseren en naar de meest dominerende soorten te benoemen.

Als eis voor de bruikbaarheid van associaties als eenheden in de vegetatiekunde werd een zekere begrensdheid van vegetatietypen gesteld. Discontinuïteiten binnen successiereeksen komen wel voor, maar bij onderlinge vergelijking van successiereeksen in brak-mineraalrijk uitgangsmilieu tot zuur-mineraalarm zien we geleidelijke overgangen. Alleen op grond van historische factoren zouden bepaalde stadia in de Zaanse en Waterlandse venen als gezelschappen onderscheiden kunnen worden. Dergelijke locale gezelschappen zijn echter wat anders dan de associaties van de Frans-Zwitserse school. Die worden volgens andere, veel subjectievere, criteria vastgesteld. Vooral het begrip constant is daarbij een struikelblok. Een verdere moeilijkheid is dat de amplituden van de soorten binnen de successiereeksen niet in alle terreinen hetzelfde zijn. De onderlinge „binding" tussen de soorten, de trouw, is niet iets vaststaands. Ook bij geografische beschouwing van vegetaties komt dat tot uiting. Het kensoortsbegrip komt daardoor op lossere schroeven. Het onderlinge verband tussen de vegetatietypen is zo sterk polydimensionaal, dat een systeem naar analogie van de idiosystematiek te verwerpen is.

Uit het opname-materiaal kan men bepaalde reeksen halen om bepaalde verschijnselen te registreren en naderhand oecologisch te onderzoeken. Op deze manier heeft het vaststellen van successiereeksen en het maken van vele opnamen zijn plaats in de vegetatiestudie.

Als zevende en laatste spreker sprak tenslotte de heer J. J. BARKMAN (Leiden) over:

Duinvegetaties van Noord-Schotland.

Op enkele plaatsen langs de rotsige kust van N. Schotland vindt men in inhammen een breed zandstrand met een smalle rij lage duintjes. Het meest interessant zijn deze duintjes bij Bettyhill, waar zij een subarctische vegetatie dragen, hoewel het klimaat er practisch vorstvrij is. De zomers zijn echter koel (gemiddelde temperatuur voor Juli 13° C., voor het gehele jaar 8° C.), er woeden 's winters hevige stormen, en aantal regendagen (240 per jaar) en gemiddelde bewolking zijn hoog; de regenval is 1000 mm per jaar. De natuurlijke boomgrens ligt er slechts 60 m boven zeeniveau.

Strand en duinen rusten bij Bettyhill op een rotssubstraat. Het strand is bij laagwater 300 à 400 m breed, de duinengordel is smal (40 tot 600 m), de duintjes zijn slechts 3 à 4 m hoog en wisselen af met langgerekte, vlakke, droge valleien, welke parallel lopen met de kust en plaatselijk veel grint bevatten (door riviertjes aangevoerd). De duinen zijn matig kalkhoudend en sterk geteisterd door konijnen, de binnenduinen ook door schapen. Er heeft duinvorming plaats.

Aan de voet der embryonale duintjes vinden we soms op het strand een gordel van *Honkenya peploides*. De duintjes worden primair gevormd door *Ammophila arenaria*, die op deze embryonale duintjes het dichtst staat en alleen hier bloeit. In het stuivende zand eronder groeien soms *Psilocybe ammophila* of *Tussilago farfara* (alleen hier). In de hierop volgende duintjes treedt onder de helm de Umbellifeer *Ligusticum scoticum* op en als zandbinder *Bryum pendulum*.

De volgende duinrijen dragen of alleen helm, of er voegen zich *Brunella vulgaris*, *Polygala vulgaris*, *Cerastium semidecandrum* en

Lotus corniculatus bij, vervolgens *Brachythecium albicans* en *Tortula ruralis* var. *arenicola*, die als zandbinders fungeren, daarna ook *Camptothecium lutescens*, en plaatselijk *Ditrichum flexicaule* var. *longifolium*, *Barbula fallax*, *Rhytidiadelphus squarrosus*, *Calliergonella cuspidata*, *Cratoneurum filicinum* var. *pseudocurvicaule* en *Galium verum*.

Tortula gaat nu gesloten tapijten vormen, waarin zich ook vestigen *Anthyllis vulneraria* ssp. *maritima* (dominant), *Plantago maritima*, *Coeloglossum viride*, *Gentiana campestris*, *Hypnum cupressiforme* var. *elatum* e.a., terwijl tegelijkertijd de helm verdwijnt. We zien vervolgens optreden *Hylocomium proliferum* en *Rhytidiadelphus triquetrus*, die een gesloten tapijt kunnen gaan vormen, onder uitsluiting van de andere mossen. *Vicia lathyroides* en *Thalictrum minus* vestigen zich in dit stadium. Door de wind of door sterke betreding in dit plantendek geslagen gaten bieden vestiging aan *Carex arenaria*, *Ononis repens* var. *mitis* en *Thymus Serpyllum* ssp. *Chamaedrys*.

De vegetatie der valleien is zeer soortenarm, soms maar met één soort, en steeds met dominantie van één soort. Dit is in de meest zeewaarts gelegen vallei *Plantago maritima*, in de daarop volgende *Carex arenaria*, met soms een heel enkele *Parnassia palustris*, en in de meest inwaarts gelegen *Thymus Serpyllum* ssp. *Chamaedrys*, die fraaie rozetten vormt met lange uitlopers, terwijl als zandbinder hier *Trichostomum crispulum* optreedt.

Op de graniethelling achter de duinen, die gegeseld wordt door de met zand beladen wind, vestigen zich als pioniers een aantal mossen, die keiharde, halfbolronde kussens vormen (tot 20 cm dik), waarin zij het zand opvangen. In de eerste plaats doet dit *Hymenostylium curvirostre*, verder *Gymnostomum rupestre*, *Grimmia conferta*, *Scapania aspera* en *Ditrichum flexicaule*. In de moskussens vestigen zich *Encalypta contorta* en *Ctenidium molluscum*, vervolgens op de moskussens *Collema* sp., veel *Saxifraga aizoides* en *Plantago maritima*. Daarna volgen *Thymus*, de arctisch-alpiene Rosacee *Dryas octopetala* en *Carex arenaria*. *Dryas* verstikt de moskussens en neemt hun zandbindende rol over. Er vormen zich miniatuurduintjes van *Dryas*, 50—80 cm. hoog en $1^1/_2$—3 m. breed, waarin de konijnen holen graven. Alleen *Thymus* weet zich te handhaven, en er komen bij: *Festuca ovina* ssp. *capillata*, *Galium verum*, *Plantago lanceolata*, *Lotus corniculatus*, *Empetrum nigrum*, *Boletus pachypus* e.a. Aan de naar de top van de helling gekeerde zijde van elke Dryasbult vestigen zich mossen, waarvan vooral *Brachythecium erythrorrhizum* als boreale soort (Scandinavië) en nieuwe indigeen voor Groot-Brittannië interessant is.

De Dryasbulten welven zich sterker, en de naar de voet van de rotshelling gekeerde zijkant wordt vrijwel verticaal. *Dryas* sterft hier af en wordt overwoekerd door *Salix repens*. Ook tussen de Dryasbulten verzamelt zich zand. Hierin vestigt zich *Pteridium aquilinum*, ofschoon het $CaCo_3$-gehalte nog 2,0% bedraagt. Alle NaCl is echter reeds uit het zand weggewassen door de regen, een bewijs voor de uitlogende werking van dit kille, regenachtige klimaat.

Plaatselijk installeert zich *Rosa spinosissima* in de zandslenken en invaheert de Dryasbulten, deze vernietigend.

Tenslotte echter vloeien de Dryasbulten ineen tot een effen, dichte, lage grasmat, sterk door schapen en konijnen afgegraasd. De zandlaag eronder is 30—100 cm dik. Een dergelijke bloemrijke, dichte grasmat, begraasd door schapen, en qua aspect te vergelijken met ons *Festuceto-Galietum maritimi*, vinden we ook op vele andere plaatsen in Schotland in de duinen; hij wordt „machair" genoemd door de Gaelische bevolking. Maar nergens draagt deze machair een arctisch karakter zoals hier.

Aan arctisch-alpiene soorten voegen zich nog bij de *Dryas*: *Polygonum viviparum*, *Selaginella selaginoides*, *Oxytropis uralensis*, *Saxifraga oppositifolia*, *Silene acaulis*, *Dichodontium pellucidum* var. *fagimontanum* en *Scapania aspera* en *aequiloba*. Behalve deze arctisch-alpiene planten vestigen zich in de Dryasmat vele gewone planten van grazige zandgrond. In totaal telde ik in één opname van 25 m^2 27 phanerogamen en 16 bryophyten. De vegetatie is dus zeer mossenrijk. Van de phanerogamen zijn nog vermeldenswaard de eu-atlantische Liliacee *Scilla verna*, verder *Primula veris*, *Listera ovata*, *Antennaria dioica*, *Linum catharcticum* en *Parnassia palustris* (op een droge zandhelling!), van de bryophyten *Mnium stellare*, *Rhodobryum roseum* en *Haplozia lanceolata*. *Festuca ovina* ssp. *capillata* breidt zich sterk uit en bereikt hier zijn optimale condities. Pas hier brengt het gras het tot bloeien. Door de sterke schapenbeweiding wordt opslag van struiken verhinderd en blijft deze Dryasmat waarschijnlijk stationnair.

Bij vergelijking van de N.-Schotse duinen met de Nederlandse valt dus in de eerste plaats op de arctische inslag in de vegetatie, vooral in die der gestabiliseerde binnenduinen, voorts een atlantische inslag (*Scilla verna*, diverse mossen) en de invloed van het vochtige klimaat in het algemeen. Het laatste uit zich in de belangrijke rol, die de mossen hier in de vegetatie spelen, in het voorkomen van hygrophiele planten op uit edaphisch oogpunt droge standplaatsen (*Coeloglossum viride*, *Parnassia palustris*, *Calliergonella cuspidata*) en van acidiphiele planten (*Pteridium aquilinum*, *Empetrum nigrum*) op betrekkelijk nog kalkrijke grond (2,0% $CaCo_3$).

Een frappant verschil met onze duinen is voorts het vrijwel ontbreken van het *Agropyretum boreo-atlanticum* in de embryonale duintjes. Waar elders langs de N.-Schotse kust *Triticum junceum* wel voorkomt, vormt deze plant dikwijls geen aparte gordel, maar is gemengd met de helm.

Merkwaardig is het voorkomen van *Ligusticum scoticum* en *Bryum pendulum* in de stuivende buitenste duintjes en van *Plantago maritima* in de buitenste valleien. Het laatste is waarschijnlijk een gevolg van het winderige klimaat en de geringe hoogte der duintjes, waardoor nog veel zeewaterdruppeltjes over de eerste kam heen vliegen. De rol van secundaire zandbinder, die bij ons *Tortella flavovirens* vervult, wordt hier overgenomen door *Trichostomum crispulum.*

Nadat Prof. HEIMANS namens de aanwezige en afwezige leden van de K.N.V.B. een woord van dank gesproken had tot Dr SCHEYGROND voor de wijze waarop hij tijdens zijn thans geëindigde zittingsperiode de diverse Nederlandse dagen voor Biosociologie en Palaeobotanie geleid heeft, sloot de voorzitter deze zeer geslaagde vergadering.

JAARVERSLAG 1948 van de Commissie voor de Bescherming van de wilde flora.

De beschermingscommissie van de Kon. Ned. Bot. Ver. is, evenals de laatste jaren, in 1948 slechts weinig op de voorgrond getreden. De Natuurbeschermingsraad, de Contactcommissie en tegenwoordig ook de afdeling Natuur- en landschapsbescherming van het Staatsbosbeheer komen bij de betrokken instanties reeds met dezelfde argumenten, die wij hebben, maar bovendien met degene die uit andere gezichtshoeken ten bate van de natuurbescherming te maken zijn. Niet, dat deze dan tezamen altijd veel succes hebben. Lang niet!

Wij mogen in Uw herinnering oproepen de lijdenshistorie van de St. Pietersberg. Het heeft aan het eind van het jaar nog even geschenen, dat de door de E.N.C.I. gevraagde concessie geweigerd zou worden en dat de vleermuizen- en handtekenings-grotten, die nog bestaan, gespaard zouden worden, evenals de coulisse langs het kanaal. Dat is echter niet gebeurd. De niet te ontkennen cementbehoefte, de industriële belangen en mogelijk ook de belangen der industriëlen hebben gezegevierd over de wensen der landschap- en groeven-minnaars. Onze commissie heeft gemeend in deze geen stem in het kapittel te moeten brengen. Tijdens de zomerexcursie van onze vereniging naar Eysden in 1924 vonden wij de St. Pietersberg reeds volkomen ontluisterd. De helling en de plateautjes aan de Maaszijde, vroeger noordelijkste standplaats van tal van zuidelijke, meest continentale planten, waren toen reeds door de Cimenteries Réunis, voorganger van de E.N.C.I., over een grote afstand afgegraven of onder zand- en grintmateriaal bedolven. Slechts weinige van de groeiplaatsen, die we van vroeger kenden, waren nog over. We hebben toen in het Ned. Kruidk. Archief deel 34 van 1925 en in Jaargang 29 van De Levende Natuur van 1924 onze waarschuwing laten horen. Bij elke gelegenheid hebben wij gezorgd dat het resterende deel van de Pietersberg bleef staan op de nominatie van Zuidlimburgse terreinen, die beschermingswaard waren. Helaas hebben wij onder deze bedrijven de botanische betekenis steeds minder zien worden. Slechts op een heel klein deel van de bestaande coulisse is nog een elk jaar weer verminderend aantal karakteristieke planten te vinden, terwijl overwoekering door de ruderaalplanten van de werkterreinen en puinberg van de E.N.C.I. die vermindering nog gaat versnellen. Bij het vergelijken van de huidige toestand en de sombere perspectieven met de vroegere toestand kwamen wij tot besluit, dat er geen aanleiding voor ons was om hoog van de toren te blazen. Moge het Belgische deel van de Pietersberg, dat toch binnenkort weer voor ons gemakkelijker toegankelijk zal zijn, ons nog lang het florabeeld geven, dat wij in Nederland er al lang hebben verloren.

Iets anders is, dat het nu meer dan ooit noodzakelijk wordt, dat de oostelijke rand van het Maasdal, van St. Geertruid tot het Missiehuis Cadier en Keer beschermd wordt. Die helling is nog in zijn oude luister. Ja, enkele uiterst zeldzame planten, karakteristiek voor het Limburgse *Querceto-Carpinetum corydaletosum*, staan er mooier dan ooit. Die hellingen en verder de streek rond Bemelen, de laatste Geulweiden met zinkflora bij Epen, moeten toch behouden worden voor op eigen streek belust Limburg en voor plantenminnend Nederland. Deze gebieden horen tot het beste wat binnen onze landsgrenzen is te vinden.

Een andere zaak trok onze aandacht in het afgelopen jaar. Onder de rook van een onzer Brabantse steden werd dit jaar een ven herontdekt, waar *Carex limosa* en *Scheuchzeria* voorkwamen in aantallen als geen onzer nog ooit had aanschouwd. Enkele ex. *Hammarbya paludosa* vulden het aan: een prachtig zuiver *Caricetum limosae*. Eerst dreigde voor dit ven een geleidelijke demping met stadsvuil en oorlogspuin. Toen dat gevaar bezworen was, kwam alarm voor een beraamde uitbaggering. Afgezien van de de kans, dat planten in kwestie dit niet zouden overleven, was er nu ook nog het gevaar dat dit bedrijf mogelijk de ondoorlatende laag onder het ven zou doorbreken, waarna het ven wel automatisch zou verdwijnen. Gelukkig is dit gevaar thans afgewend. Eigenaars en beheerders zijn door bemiddeling van verschillende relaties ingelicht en zullen alles doen wat mogelijk is om het voortbestaan van ven en vegetatie te verzekeren.

Nog een ander punt moeten wij hier onder de aandacht van bestuur en leden van de K.N.B.V. brengen en wel de steeds verder gaande bestrijding van onkruiden met groeistoffen en kleurstoffen. Bij de zomerexcursie van 1947 naar de N.O.-polder zagen wij het resultaat: schone akkers zonder enig onkruid. Onze commissie kan zich voorstellen, dat men voor het groot-landbouwbedrijf veel van deze methode verwacht. Maar zij vreest toch, dat men bij het besproeien van de akkers ook aan de omgeving wel een portie van deze stoffen zal toedienen. Zo maakt onze commissie zich wel bezorgd voor de vaak zeer interessante vegetatie van slootkanten en dijkbermen, die de akkers omgeven. Mogelijk willen onze leden, die de proefnemingen met groeistoffen in het veld leiden, dit eens onder de ogen zien. Misschien is er een methode te vinden, die deze stoffen binnen de ermee te behandelen perken houdt.

De Secretaris,
B. o. Z., Dec. 1948. JAN G. SLOFF.

VERSLAG van de Commissie voor de Phytopathologie over 1948.

In de vacature, ontstaan door het periodiek aftreden van Dr J. C. 's JACOB werd voorzien door de verkiezing van Dr C. WEHLBURG. Deze laatste trad in najaar 1948 af wegens vertrek naar Argentinië.

In dit jaar heeft de Commissie één vergadering gehouden en wel op 24 April te Utrecht, waarbij gesproken werd door Dr J. GROSJEAN over het onderzoek naar de loodglansziekte en Ir J. W. SEINHORST over de invloed van de grond op de aantasting van planten door stengelaaltjes. In het najaar 1948 is de kwestie van de contribuanten definitief geregeld in overleg met het Bestuur van de Kon. Ned. Bot. Ver.

De Secretaresse,
CAROLINE H. KLINKENBERG.

VERSLAG van de Commissie voor de Plantenphysiologie over het jaar 1948.

In Januari 1948 werd in de vacature ontstaan door het aftreden van Mej. Dr A. A. KLEINHOONTE, die niet herkiesbaar was, voorzien door de verkiezing van Mej. Dr C. J. GORTER.

In het afgelopen jaar werden twee bijeenkomsten gehouden. De eerste vond plaats op Zaterdag 8 Mei in het Botanisch Laboratorium te Leiden; voordrachten werden gehouden door Mej. Dr M. A. DE VRIES over „De vorming van phytomelaan bij *Tagetes patula* en enige andere Composieten" en door de heer G. KAMERBEEK over „Dwerggroei en peroxydasegehalte". Aanwezig waren 19 leden. De tweede bijeenkomst werd gehouden op Zaterdag 29 Mei in het Botanisch Laboratorium te Groningen; spreker was Dr T. ALBERDA, de voordracht handelde over „De phosphaatopname door maisplanten"; aanwezig waren 14 leden en 2 introducé's.

De derde vergadering, die in December gehouden zou worden, moest worden afgelast wegens ziekte van de spreker.

De Secretaris,
A. W. H. VAN HERK.

VERSLAG van de Commissie voor Plantensystematiek en -geografie over 1948.

Door de Commissie werd op 13 Juni een dagexcursie naar Voorne georganiseerd, ter inleiding van het nomenclatorisch congres dat te Utrecht van 14—19 Juni werd gehouden. Buitenlandse deelnemers waren: E. D. MERRILL (Am.), F. R. FOSBERG (Am.), H. W. RICKETT (Am.), J. RAMSBOTTOM (Eng.), T. A. en mrs. M. L. SPRAGUE (Eng.), H. HUMBERT (Fr.), W. ROBYNS (Belg.), C. SKOTTSBERG (Zwed.), N. HYLANDER (Zwed.), miss C. M. EARDLEY (Austral.), D. CHATTERJEE (Ind.). Door dit vrij grote aantal kon de Nederlandse deelneming aan deze excursie slechts beperkt zijn. De heer C. SIPKES leidde het gezelschap rond langs Quackjeswater en Nieuwe Water; de lunch, aangeboden door het Administratiefonds Rotterdam, werd gebruikt in de Volkshogeschool te Rockanje.

Op 23 October vond een bijeenkomst plaats in het Botanisch Laboratorium te Utrecht. Aantal aanwezigen 33. Daar bij de benoeming van een opvolger van Dr PULLE als commissielid nog niet was bepaald wie de functie van voorzitter zou bekleden, werd dit ter vergadering gedaan. Dr H. J. LAM is thans voorzitter. In de plaats van Dr CH. H. ANDREAS zal aan het Algemeen Bestuur Dr F. P. JONKER worden voorgesteld als Commissielid. Als zijn benoeming wordt goedgekeurd, zal hij de functie van secretaris vervullen.

Op de vergadering werden voordrachten gehouden door Dr C. G. G. J. VAN STEENIS over de opzet van de Flora malesiana, Dr H. J. LAM over Plantenarealen in de westelijke Stille Oceaan, Dr H.

C. D. de Wit over „Iets uit het leven van Spanoghe”, Dr R. C. Bakhuizen v. d. Brink over adventieven.

Wegens afwezigheid der meeste commissieleden aan het einde van de vergadering werd deze gesloten door Dr Ir A. W. Kloos. Daarna was er echter voor belangstellenden nog gelegenheid tot het bezien van diens herbariummateriaal van *Amaranthus* en oude boekwerken van W. van Dijk.

De Secretaresse,
Groningen, Januari 1949. Ch. H. Andreas.

NOTULEN over 1948.

JAARVERGADERING op Zondag 1 Februari 1948 in het Botanisch Laboratorium te Utrecht.

Aanwezig zijn 2 introducé’s, nl. de heren W. van Zeist en P. Stoutjesdijk en 47 leden, de dames en heren: Andreas, Arisz, Badenhuizen, Bels-Koning, A. J. Bianchi, S. de Boer, van Asperen de Boer, Bottelier, Gonggrijp, A. Gorter, Hartsema, Heimans, van Herk, Houwink, Jaarsveld, ’s Jacob, P. Jansen, Jaspers, Jonker, Karstens, Kern, Kloos, Koningsberger, G. Kruseman, van der Laan, Lam, Lanjouw, J. C. Lindeman, Nieuwenhuijsen, van Os, de Bruyn Ouboter, Piet, Roodenburg, Scheygrond, Sloff, van Slogteren, van Soest, van Steenis, Stomps, Varossieau, P. Vermeulen, Waterbolk, Weevers, Went, Westerdijk, Wijbrans, R. van der Wijk, Zaneveld.

In zijn openingswoord herdenkt de Voorzitter, Dr W. H. Arisz, de leden, die de Vereniging in 1947 door de dood ontvielen: Mej. Dr Jantina Tammes, hooglerares te Groningen. De Vereniging heeft veel aan haar te danken: in de Commissie voor de redactie van het Recueil des Travaux Botaniques bekleedde zij verscheidene jaren het secretariaat en het voorzitterschap. Ook overleed de heer Joh. Jansen, bekend florist uit het land van Nijmegen; en Dr J. J. Smith, kenner van de tropische Orchideeën, autodidact en Doctor honoris causa; voorts de heer F. van der Wouw, candidaat in de biologie en assistent aan het Botanisch Laboratorium te Utrecht. De Vereniging houdt hun aller nagedachtenis in ere. De Voorzitter bespreekt dan de toestand inzake de tijdschriften. Het is in 1947 nog niet mogen gelukken de achterstand van de oorlog geheel in te halen; men is echter op de goede weg en het is te hopen, dat de tijdschriften in 1948 geheel „bij” zullen geraken. Tenslotte wijst de Voorzitter op het belang van een bloeiende wetenschappelijke vereniging voor de Botanie in Nederland; hij wekt daarom op tot trouw aan de vereniging, vooral ook die leden, die door omstandigheden slechts een losse band met de vereniging onderhouden.

De notulen van de vorige vergadering worden voorgelezen en goedgekeurd.

Voorts worden voorgelezen de ontwerp-jaarverslagen van de eerste Secretaris en van de permanente Commissies. Het ontwerp-jaarverslag van de Commissie tot Bescherming van de wilde Flora vermeldt, dat het Beerse-dal, niettegenstaande de gevoerde actie, ontgonnen zal worden en dus verloren is. Dr WEEVERS vult hierbij aan, dat een stuk ervan reeds lang tot natuurreservaat verklaard is: de poging om een aangrenzend terrein eveneens te reserveren en daardoor de blauwgrasland-associatie beter te beveiligen door haar een ruimer gebied te geven, is echter mislukt.

De Penningmeester brengt verslag uit van zijn beleid in '47. Evenals het vorig jaar laat hij op verschillende punten een somber geluid horen: De contributie der leden in Indonesië kan niet overgemaakt worden en is dus onzeker. Een belangrijk bedrag (*f* 290.—) is oninbaar; het zijn contributies van 6—7 jaar geleden van leden uit Indië en uit het buitenland, die na de oorlog hun lidmaatschap niet hebben voortgezet. Lang niet alle rente is nog bijgeschreven; er zal zeker renteverlaging zijn. De Penningmeester dringt op bezuiniging aan van de drukkosten en porti der convocaties. Men kan oproepen voor vergaderingen, die ongeveer terzelfder tijd vallen, combineren. De prijzen voor de dissertaties in het Recueil zullen verhoogd moeten worden, daar de drukkosten belangrijk gestegen zijn. Hij wekt de leden op, delen van het Recueil te kopen; het is thans nog goedkoop. Hij verzoekt de medewerking der leden om hem de vele moeilijkheden bij het innen der contributies te besparen en vraagt om de bijdragen voor de Flora Neerlandica wederom te betalen.

Naar aanleiding van de begroting voor 1948 worden enkele vragen gesteld: Dr KONINGSBERGER informeert naar het bedrag der subsidie voor het C.B.S.; hij zou de band der vereniging met dit instituut niet gaarne verloren zien gaan. Het vorig jaar is in overleg met Dr WESTERDIJK het bedrag echter al op *f* 100.— teruggebracht, daar de financiële toestand van het C.B.S. dit op het ogenblik toelaat. Dr WEEVERS informeert naar het Wahlenbergia-terrein. — Een bedrag is hiervoor uitgetrokken.

De nieuwe leden, genoemd op het convocatiebiljet, worden bij acclamatie benoemd. Bovendien de volgende aspirant-leden, die op de vergadering worden voorgesteld, (onder dispensatie van artikel 6, 1e lid der statuten): de heren R. J. D. DOORENBOS en M. WITKAMP door de leden BEUMÉE, VENEMA en WESTHOFF; de heer A. MIDDELHOEK door de lepen HEIMANS, KERN en MÜLLER; Mej.

A. KAMPS door de leden ANDREAS, ARISZ en VAN DER WIJK. Als student-lid de dames en heren: Mej. M. LUCARDIE door de leden HEIMANS, VAN HERK en MÜLLER; C. O. DWARS door de leden HEIMANS, MÜLLER en P. VERMEULEN; P. VAN ROYEN, B. HUISINGA, E. A. MENNEGA, T.STOFFERS, P. STOUTJESDIJK, H. J. SWART door de leden JONKER, LANJOUW en J. C. LINDEMAN. Tenslotte als gecombineerde leden met de Nederl. Dierkundige Vereniging de dames en heren: Mej. A. K. KREMER, Mej. W. TERPSTRA, Mej. E. VAN DEN BROEK, W. VAN ZEIST, J. F. ROBORGH, PH. SEDEE en G. MEYER door het Bestuur.

Alle leden der permanente Commissies worden benoemd, zoals zij voorgesteld zijn op het convocatie-biljet.

De benoeming wordt bekrachtigd van enkele leden voor de redactie van de Flora Neerlandica. Deze hebben hun functie reeds enige jaren vervuld; door de oorlogsomstandigheden konden zij echter nog niet officiëel door een vergadering van de leden aangesteld worden. In de redactie van de Flora Neerlandica hebben thans zitting: Dr TH. WEEVERS, Dr J. HEIMANS, Dr S. J. VAN OOSTSTROOM en Dr Ir A. W. KLOOS. Dr HEIMANS deelt namens de redactie mede, dat thans een eerste deeltje van de Flora zal verschijnen; dit dient tevens als proefuitgave. Het zal de Gymnospermen en Pteridophyten behandelen en 6 vel (= 100 blz.) omvatten. Voor leden zal de prijs vermoedelijk *f* 3.75 bedragen; voor niet-leden der K.N.B.V. *f* 6.50. Op een vraag van Dr VAN ASPEREN DE BOER antwoordt Dr HEIMANS, dat de omvang vrij groot is: iedere soort heeft meer dan een bladzijde.

Thans volgt de schriftelijke stemming over een bestuurslid in de vacature Dr BELS-KONING. Aanwezig zijn 47 leden; uitgebracht worden 47 stemmen, waarvan 32 op Dr JAARSVELD, 12 op Dr DE ZEEUW en 3 blanco. Mejuffrouw Dr A. JAARSVELD is dus benoemd. Desgevraagd verklaart zij de benoeming aan te nemen. De Voorzitter dankt Mevr. BELS-KONING voor haar medewerking in het Bestuur.

Om 11.45 houdt Dr W. H. ARISZ zijn jaarrede, getiteld: „In open vaarwater". De tekst van deze rede is reeds gepubliceerd in het Nederlandsch Kruidkundig Archief, deel 56, blz. 73.

Om 12.30 wordt de vergadering geschorst voor de koffiemaaltijd in het Universiteitshuis.

Om 14 uur volgt de wetenschappelijke vergadering. Hier zijn aanwezig 57 leden; erbij gekomen zijn de dames en heren: BEUMÉE, G. BRINK, J. G. DE BRUIJN, P. A. FLORSCHÜTZ, J. LAARMAN, LÖHNIS, LENS, MENNEGA, VAN OOSTSTROOM, RIJVEN, VAN ROYEN, SALVERDA, DE WAARD, WASSINK, WESTHOFF, WIERINGA, DE ZEEUW.

De eerste voordracht wordt gehouden door Dr A. A. PULLE over:

De Ontwikkeling van het Botanisch Onderzoek in Suriname.

In de geschiedenis van het botanisch onderzoek kunnen drie perioden worden onderscheiden. Aanvankelijk stelde men zich onder invloed van LINNAEUS ten doel, zo veel mogelijk exotische planten te verzamelen van alle delen der aarde, die bereikbaar waren. Van ongeveer 1750—1775 is er bijzondere belangstelling voor Suriname geweest van de zijde van LINNAEUS en zijn leerlingen. Verzamelaars uit die tijd zijn de Zweden ROLANDER en DAHLBERG en de Nederlander van Zwitserse afkomst ALLAMAND. Auteurs waren: LINNAEUS, ROTTBOELL en ROLANDER.

In de tweede periode, die van 1820—1860 loopt, werd ernaar gestreefd zoveel mogelijk planten van Suriname te leren kennen, doch zonder het doel een Flora van het land te maken. Uit deze tijd stammen de eerste algemeen verspreide en goed bewerkte collecties, zoals die van HOSTMAN, KAPPLER, KEGEL, WULLSCHLÄGEL, FOCKE en SPLITGERBER. Aan hun bewerking hebben een groot aantal zeer bekende botanici deel genomen, b.v. F. A. W. MIQUEL.

De derde periode begint in 1900 met de eerste van een serie wetenschappelijke expedities. Hun botanisch materiaal is verwerkt in sprekers dissertatie van 1906; een soort van prodromus van de Flora van Suriname. Daarbij sluiten zich aan: particuliere reizen van hemzelf, van Dr LANJOUW en enkele andere reizigers en de werkzaamheid van het Boswezen, dat zeer grote verzamelingen heeft bijeengebracht. Al deze collecties moesten de bouwstoffen leveren voor een Flora van Suriname. In 1932 is hiermede een begin gemaakt. Ongeveer drie kwart van het in het Engels geschreven werk is thans verschenen. De uitgave wordt gefinancierd door het VAN EEDEN-fonds.

Spreker behandelt vervolgens de oprichting van de Natuurwetenschappelijke studiekring voor Suriname en Curaçao in Augustus 1945, die ten doel heeft alle onderzoekingen op dit gebied te coordineren. Op het programma staat onder meer: het uitrusten van een botanisch-zoölogisch-geomorphologische expeditie in 1948—1949, waarbij de samenwerking van de drie vakken op de voorgrond staat. Een tweede belangrijk programmapunt is: het maken van een beschrijving van de boomsoorten van Suriname, in welke beschrijving tevens zal worden opgenomen de anatomische bouw van het hout. Zowel voor dit werk, als voor het verder bewerken van de Flora van Suriname is afzonderlijke assistentie verkregen. Spreker zegt woorden van dank tot zijn vele medewerkers.

Na enige discussie over nog weer andere dan de vele, door DR

Pulle reeds genoemde, onderzoekers, zegt de Voorzitter de spreker dank en gaat men over tot de volgende voordracht.

Dr P. Vermeulen spreekt over:

De Splitsing van het Geslacht Orchis.

Het geslacht *Orchis* behoort tot de *Monandrae*, de *Orchidaceae* met één enkele meeldraad en tot de groep van de Ophrydeeën (de oudste naam; van Lindley afkomstig) of *Basitonae Pfitzer*, zo genoemd naar de bevestiging van de pollinia, die met hun bases aan de hechtschijfjes vastgroeien. Deze hechtschijfjes vormen met het hen soms omhullende beursje een deel van de derde stempellob, het rostellum.
het geslacht *Orchis* nagegaan. Linnaeus noemde de lip „nectarium" en hij onderscheidde een onder- en een bovenlip; de laatste had hij nodig als omhulling van de polliniën, die hij als meeldraden beschouwde. Dit is de reden, dat wij in het werk van Linnaeus de Orchideeën onder de *Diandria* gerangschikt vinden. Adanson en later Schwartz verdedigen de mening, dat er slechts één meeldraad is. Door het werk van Brown en Richard, die de merkwaardige bouw van het rostellum ontdekken, en Klinge, die bewust of onbewust de Amerikaanse soorten van het geslacht *Orchis* uitsloot, heeft het genus de grenzen gekregen, die men er in de flora's aan toekent. Klinge onderscheidde twee subgenera: *Euorchis* met ronde — en *Dactylorchis* met handvormige knollen.

Er werd nu nagegaan, of het geslacht *Orchis* wel een eenheid vormt. Aan de hand van de ontwikkeling van de kiemplant en de bouw van de knol blijkt, dat de geslachten met handvormige knollen (*Gymnadenia*, *Nigritella*, enz.) samen met het subgenus *Dactylorchis* een eenheid vormen tegenover de geslachten met ronde of ovale knollen, zoals *Aceras*, *Ophrys*, enz. samen met het subgenus *Euorchis*. Deze eerste indruk wordt versterkt door de vorm van de bracteeën, de habitus van de planten en het chromosomen-garnituur. Bovendien blijkt uit een literatuurbespreking, dat de rondknollige geslachten onderling en de geslachten met handvormige knollen onderling gemakkelijker bastaarderen dan de soorten van de subgenera *Euorchis* en *Dactylorchis*.

Dit alles voert logisch tot de opvatting, dat het geslacht *Orchis* verdeeld dient te worden in twee geslachten en wel: *Orchis* Linnaeus emend. Vermeulen en *Dactylorchis* (Klinge) Vermeulen.

Na afloop der discussie sloot de Voorzitter onder dankzegging aan de sprekers de vergadering.

LEDENVERGADERING op Zaterdag 29 Mei 1948 in het Botanisch Laboratorium te Groningen en excursie naar de Hortus De Wolf en het Lheebroekerzand op Zondag 30 Mei 1948.

Op de vergadering van Zaterdagavond 29 Mei zijn aanwezig 11 introducé's, nl. de dames en heren: Mevr. Arisz-Sabron, Mej. Baggerman, P. Bruin, Mevr. Clason-Laarman, Mevr. van Dijk-Koopmans, Heikens, Kamps, Peerlkamp, Mej. Post, Prop en Mej. van Rooyen; voorts 63 leden, nl. Alberda, van Andel, Andreas, Arisz, Badenhuizen, Bakker, Berger, A. T. J. Bianchi, S. de Boer, J. Oortwijn Botjes, Brand, Bremer, Bremer-Reinders, Brink, Engelen, van Eyndhoven, Evenhuis, Feekes, Maas-Geesteranus, Goedewaagen, A. Gorter, C. J. Gorter, Harmsen, Heimans, Helder, van Herk, van den Honert, Honing, Houwink, s' Jacob, C. Th. A. de Jongh, Jonker, Kamerbeek, J. Kuyper, Laarman, Lam, Lanjouw, F. M. Muller, van Nie, Oomen, van Ooststroom, van Os, van der Paauw, ter Pelkwijk, Pool, Pulle, A. F. M. Reijnders, Rijven, Roelofsen, Salverda, Sirks, Van Slogteren, Van Steenis, van der Veen, Vermeulen, van Borssum Waalkes, Waterbolk, van der Wijk, Wilbrink, Wildervanck, en 3 onleesbaar.

De Voorzitter, Dr W. H. Arisz, opent de vergadering en heet de aanwezigen welkom in Groningen na ± 10 jaar. Hij spreekt daarbij de mening uit, dat het eens in de 10 jaar wel de moeite waard is naar Groningen te komen. Vooral de nieuwe Hortus de Wolf zal blijken de moeite te lonen!

De notulen van de vorige vergadering worden voorgelezen en goedgekeurd.

De Voorzitter deelt mede, dat met de Ned. Dierk. Ver. nog nader overleg moet worden gepleegd over de gemeenschappelijke leden en de te betalen contributie. Wij (de Kon. Ned. Bot. Ver.) hebben studentleden en gecombineerde leden; de Ned. Dierk. Ver. heeft alleen gecombineerde student-leden. Dit moet tot overeenstemming gebracht worden. De vergadering laat het aan het Bestuur over dit te regelen.

Het aspirant-lid, A. Récourt, voorgesteld op de convocatie, wordt bij acclamatie benoemd; eveneens de volgende aspirant-leden, die door het Bestuur op de vergadering worden voorgesteld (met dispensatie van artikel 6, 1e lid, der Statuten): F. I. Brouwer, Dr B. J. Cholnoky, J. C. Lodder, O. P. Mechelinck, R. Peelen.

Dan brengt de Voorzitter het bestuursvoorstel om Prof. Dr A. Frey-Wyssling te Zürich tot corresponderend lid voor te dragen. Prof. Frey-Wyssling heeft lange jaren in N.O.I. gewerkt en onder-houdt veel en gaarne contact met Nederland. Volgens artikel 7 der Statuten zijn 10 ondertekeningen van leden vereist voor het voorstellen van een corresponderend lid. De Voorzitter laat het voorstel circuleren, de aanwezigen tekenen.

Daarna wordt overgegaan tot het wetenschappelijke gedeelte.

Eerst spreekt Dr F. VAN DER PAAUW over:

Invloed van de watervoorziening op de ontwikkeling en de opbrengst van haver.

Nagegaan is welke invloed een wijziging in de watervoorziening, in het bijzonder het optreden van droogte, heeft op de stofproductie en de lengtegroei van blad en stengel van het zich ontwikkelende gewas. Verder is de invloed bepaald, die in verschillende stadia van de ontwikkeling invallende droogteperioden op de vorming van de opbrengst hebben. Het blijkt, dat sterke verdroging weliswaar belangrijk bladsterven veroorzaakt, maar noch de stofproductie, noch de groei van stengel en van het jongste blad tot stilstand brengt, integendeel herstellen deze zich na korte tijd. Als na een droogteperiode weer water ter beschikking komt blijkt het gewas, vooral in vroege stadia, in staat de ontstane achterstand ten dele weer in te halen. Droogte tijdens het doorschieten belemmert echter de stengelgroei, een dergelijk gewas blijft zeer kort.

De schade, welke de opbrengst door droogte lijdt, is enigszins verschillend voor stro en korrel. De opbrengst van het eerste lijdt het sterkst door betrekkelijk vroeg optredende droogte, van het laatste door een droogteperiode tijdens de bloei, in welk geval minder korrels tot ontwikkeling komen.

De verdamping van het gewas neemt in sterke mate toe bij stijging van de temperatuur, deze toename is relatief sterker dan de toename van de verdamping van een vrij verdampend wateroppervlak. Een invloed van de belichtingssterkte op de verdamping is weliswaar aantoonbaar, maar van vrij ondergeschikt belang, de windsterkte heeft in het geheel geen invloed.

Het verdampend vermogen van het gewas is het grootst kort voor de beëindiging van de bladgroei.

De verdamping blijkt voornamelijk door de grootte van het verdampend oppervlak, en binnen ruime grenzen slechts weinig door het vochtgehalte van de grond bepaald te worden.

Het verschil tussen op droge en op natte grond gegroeid gewas is reeds vroeg, wellicht reeds tijdens de kieming, ontstaan. Later assimileert het eerstgenoemde echter sterker, zodat de achterstand relatief wordt ingehaald.

De temperatuur heeft niet alleen sterke invloed op de verdamping, maar ook op de stofproductie. Warm droog weer is zeer schadelijk als er onvoldoende water is. Het bladoppervlak wordt dan in sterke mate gereduceerd, terwijl tevens de mogelijkheid voor het gewas verloren gaat om van de gunstige temperatuur gebruik te maken voor de stofproductie.

Vervolgens houdt Dr R. VAN DER WIJK een *demonstratie van stereoprojectie*, afwisselend voor twee groepen van telkens circa 36 personen.

Hij laat zien opnamen van vegetaties in de Hortus en buiten, en geomorphologische photo's, ten dele tegelijk met stereocamera, ten dele na elkaar met enkelvoudige camera opgenomen; de laatste mislukken bij sterke beweging door wind, e.d. De eerste worden met dubbele projector over elkaar heen geprojecteerd met onderling loodrecht op elkaar gepolariseerd licht en bekeken met brillen (voor iedere toeschouwer) met polaroid-film op de glazen loodrecht op de polarisatierichtingen.

De twee projectoren moeten ten opzichte van elkaar verschoven kunnen worden in verband met verschillende verhouding van objects-afstand, opnamebasis en brandpuntsafstanden.

Voordeel tegenover anaglyphen is: opname en projectie in originele kleuren, zwart, bruin of kleurenphoto's in natuurlijke kleuren!

Tenslotte houdt de heer E. LAARMAN zijn voordracht:

Inleiding tot het bezoek aan de Hortus de Wolf te Haren.

Het terrein de Wolf beslaat een oppervlakte van ruim 12 ha Slechts het gedeelte, dat vóór 1945 is tot stand gekomen, zal worden bezocht en wel het loofhout- en het naaldhoutgedeelte van het arboretum en de hierbij aansluitende zgn. natuurlijke kweekplaatsen.

In dit laatstgenoemde gebied wordt getracht, aan planten, die niet of moeilijk achter een etiquet te kweken zijn, gunstige ontwikkelingsvoorwaarden te geven. De planten zijn: wieren, schimmels, korstmossen, levermossen, bladmossen, Orchidaceae, Lycopodiaceae, vele Ericaceae en ook uit andere families, planten met een zeer geringe tot geringe stofproductie, zowel uit ons als uit ander klimaatsgebied, zoals b.v. alpine en subalpine weide- en rotsplanten.

De omstandigheden worden natuurlijk gehouden; nadat het bodemrelief is aangebracht, wordt generlei bewerking meer in de bodem toegepast. Door de invloed van het bodemrelief ontstaat een gedifferentieerde flora; door de menselijke invloed moet ze in stand worden gehouden.

Teneinde de ontwikkeling van planten met grotere stofproductie tegen te gaan, wordt op verschillende wijzen krachtig in de ontwikkeling van de vegetatie ingegrepen. Door deze wijze van werken krijgen de genoemde planten uitbreidingsmogelijkheid. Nu en dan wordt gelegenheid gegeven tot nieuwe vestiging, door op verschillende plaatsen de gehele vegetatie te vernietigen.

Steeds wordt de menselijke invloed uitgeoefend volgens een bepaald schema.

De excursie wordt in deze tijd van het jaar gehouden, omdat o.a. de volgende soorten rijkelijk bloeien: *Orchis mascula*, *O. militaris*, *O. Morio*, *O. majalis*, *O. laxiflora*, *Listera ovata*, *Pinguicula vulgaris*, *Cornus suecica*, *Pyrola minor*.

Op Zondag 30 Mei wordt de excursie gehouden naar de Hortus De Wolf en het Lheebroekerzand. Er zijn in totaal 59 deelnemers, leden, leiders en introducé's. De excursie wordt gehouden per autobus en particuliere auto (van VAN SLOGTEREN).

Om 8.30 uur vertrekt men van het Zuiderdiep naar Haren, waar onder leiding van de heren VAN DER WIJK, LAARMAN en VAN BORSSUM WAALKES en Mej. ANDREAS een bezoek wordt gebracht aan de Hortus De Wolf, met o.a. *Orchideeën*, *Pinguicula*, *Cornus suecica*, e.a.. Alle deelnemers zijn zeer enthousiast.

Dan wordt de tocht per bus en auto voortgezet naar Oudemolen en gaat men verder te voet, onder leiding van VAN DER WIJK, WATERBOLK en VAN BORSSUM WAALKES langs de Drentse Aa en Anloër Diepje naar Gasteren. Men ziet hierbij o.a. *Phyteuma nigrum*, *Orchideeën*, *Crepis paludosa*, *Chrysosplenium alternifolium*, *Carex pallescens*.

Na een goede lunch in Hotel Wesseling te Dwingelo rijdt men naar het Lheebroekerzand, waar wordt gewandeld onder leiding van VAN DER WIJK en Mej. TER PELKWIJK. Interessant zijn hier de Juniperusvegetaties en de vennen met verschillende Sphagnumsoorten, *Oxycoccus*, enz.

Tenslotte rijdt men met bus en auto naar station Beilen, waar, na een dankwoord van de Voorzitter aan de verschillende leiders, deze interessante excursie wordt beëindigd.

LEDENVERGADERING op Zaterdag 23 October 1948 in het Botanisch Laboratorium te Utrecht.

Aanwezig zijn twee introducé's, nl. Prof. en Mevrouw PRINGSHEIM uit Cambridge, en 44 leden, de dames en heren: ANDREAS, ANKER, ARISZ, A. J. BIANCHI, BOTTELIER, BAKHUIZEN VAN DEN BRINK, DULLEMEIJER, MAAS GEESTERANUS, A. GORTER, HARTSEMA, VAN HATTUM, HEIMANS, VAN HERK, VAN DEN HONERT, HOUWINK, JAARSVELD, JONKER, KARSTENS, KLOOS, KOK, MANTEN, MARQUENIE, MENNEGA, VAN OOSTSTROOM, TER PELKWIJK, ROODENBURG, P. VAN ROYEN, J. C. SOBELS, SPIERENBURG, VAN DER STEEN, STOMPS, THOMAS, VERMEULEN, VROMAN, VAN BORSSUM WAALKES, WEEVERS, H. C. DE WIT, R. VAN DER WIJK, DE ZEEUW en vijf onleesbaar.

De voorzitter, Dr W. H. ARISZ, opent de vergadering en spreekt een bijzonder woord van welkom tot de gast van deze avond, Prof. E. G. PRINGSHEIM.

Nadat de notulen van de zomervergadering met excursie op 29 30 Mei zijn voorgelezen en goedgekeurd, wordt overgegaan tot het benoemen van enkele nieuwe leden. De per convocatie voorgestelde leden DULLEMEIJER, Mej. VAN HEES, MARQUENIE, Dr Ir MULDER en Mej. ROOYMANS worden alle bij acclamatie benoemd, evenals de heer DE WILDE, die met dispensatie van art. 6, 1e lid, der Statuten, staande de vergadering wordt voorgesteld door de leden HEIMANS, KLOOS en VLIEGER.

Ook de benoeming van Prof. Dr A. FREY-WYSSLING te Zürich tot corresponderend lid wordt bij acclamatie goedgekeurd.

Vervolgens doet de Voorzitter mededeling van enkele binnengekomen circulaires, waarvan voor de leden exemplaren verkrijgbaar zijn, voorzover de voorraad strekt.

De eerste behelst een uitnodiging tot deelneming aan het 2nd International Congress of Crop Protection, hetgeen van 21—28 Juli 1949 te Londen gehouden zal worden.

De tweede bevat een uitnodiging van de Society for Experimental Biology aan de Nederlandse zoölogen en botanici voor het bijwonen van de 75e Conference of the Society, te houden te Oxford op 6, 7 en 8 April 1949. Deze bijeenkomst samen met Nederlandse experimentele biologen wordt gehouden ter reciprocering van het zeer geslaagde congres te Utrecht in April 1947.

Daarna wordt overgegaan tot de voordrachten.

De eerste spreker is Dr H. J. LAM, met een voordracht over:

Stachyosporie en Phyllosporie als basis voor een systeem.

In zijn inleiding behandelde spr. allereerst het mogelijke grondplan der Cormophyten (incl. de Bryopsiden) als één natuurlijke groep en vervolgens de klaarblijkelijke tendenties volgens welke zij zich, in verband met de milieuwisseling water-land hebben ontwikkeld. Met de interessante regressieve orthogenesen der gametofyt gaat een niet minder interessante reeks progressieve orthogenesen van de sporofyt gepaard. Daarbij treden als voornaamste tendenties aan de dag, verbetering der organische voeding door oppervlakte-vergroting (vervanging der dichotome vertakking door andere vertakkingsvormen; enatiebladeren; teloombladeren), bescherming der vegetatieve knoppen door binding aan bladeren (blad- en takstand), en bescherming der voortplantingsorganen, met name der sporangiën (later vooral de vrouwelijke). T.a.v. de laatstgenoemde tendentie onderscheidt spr. twee gevallen: a) *stachyosporie*, waarbij de sporangia zelfstandige telomen, dus assen blijven en de beschermingstendentie zich uit door secundaire binding aan bladeren (stegofyllen); en b) *fyllosporie*, waarbij gemengde syntelomen optreden met overwegend steriele telomen, zodat echte sporebladeren ontstaan met de sporangia eerst nog aan de randen, later laminaal. Bescherming der sporangiën kan b.v. tot stand worden gebracht door het binnenwaartse omvouwen der bladranden, maar ook op andere wijze. Daar er gradatie bestaat in gemengde telomen, is de grens tussen de twee typen niet scherp; fyllosporie is uiteraard de afgeleide toestand.

Spr. gaat dan na welke invloed deze blijkbaar evolutionnair belangrijke processen op de systematiek kunnen hebben. Bryopsiden, Psilopsiden (incl. de Psilotales), Lycopsiden en Sphenopsiden zijn blijkbaar geheel stachyospoor; ook de Protangiospermen (Gnetales en Casuarina). De Pteropsiden (Varens) zijn geheel of bijna geheel fyllospoor. De Cycadopsiden en Coniferopsiden echter zijn op dit punt blijkbaar van gemengde aard. Terwijl de Cycadales geheel fyllospoor schijnen te zijn, zijn de ♂ organen der Bennettitales en Coniferales merendeels fyllospoor, de ♀ daarentegen merendeels stachyospoor. Hierbij doen zich nog opmerkelijke complicaties voor, b.v. bij de Pinaceae, waarbij zich een secundair cladosporofyl heeft gevormd. Ginkgo is kennelijk in beide geslachten stachyospoor: van vruchtbladresten is geen sprake.

Uitvoeriger gaat spr. dan in op de toestand bij de Angiospermen. De voorlopige indruk is, dat het beginsel hier weer scherper opgaat. Stachyospoor zouden dan zijn de meeste Monochlamydeeën, de Plumbaginales en Primulales en wellicht sommige Monocotylen (Pandanales, Spadicifloren) en Dialypetalen (b.v. de Columniferen c.s.). Bij dit type zijn de bloemen veelal klein en de ♂ en ♀ sporangioforen (geen sporofyllen) zijn er als het ware op bijkomstige wijze door omhuld. Bij beide geslachten zijn zij vaak axillair gebonden aan stegofyllen (tepalen, c.q. pseudocarpellen) en hun stelen (filament, funiculus) vertonen nog sporen van dichotomie en soms zelfs van een orgaantje, dat aan een hoekblad doet denken. Alleen bij de Centrospermen en afgeleiden komt het tot kransstand, kelk en kroon, grote bloemen, onderstandig vruchtbeginsel en sympetalie.

Fyllospoor zouden dan de overige groepen zijn; het prototype vindt men in de Polycarpicae. De bloemen zijn in beginsel groot en dragen echte micro- en macrosporofyllen met ongestoorde alternantie. Sporen van dichotomie vindt men vooral in de bladnervatuur.

Een voorlopig nader onderzoek leert echter, dat zeer vele groepen op dit beginsel nader getoetst moeten worden en dat diepgaand ontogenetisch, anatomisch en cytologisch onderzoek nodig is, om de „nieuwe morfologie" der Angiospermen te leren begrijpen. Spr. verwacht hiervan grote resultaten voor de phylogenie en de systematiek. Hij vermoedt, o.a. op grond van de uniformiteit van embryozak en meeldraden, dat de Angiospermen als groep wel een gemeenschappelijke afstamming kunnen hebben, maar die moet dan liggen vóór de scheiding in stachyo- en fyllospoor en dus zeer oud zijn. Wellicht moet men de stamgroep zelfs zoeken bij de oudste, wellicht Devonische Pteridospermen, maar de Angiospermen-potentie moet dan wel lang latent zijn gebleven. De huidige groep schijnt echter op zijn minst birheitrisch.

Vervolgens sprak Dr A. MANTEN over:

Phototaxis van Purperbacteriën.

De phototactische verschijnselen bij de purperbacterie *Rhodospirillum rubrum* vormde het onderwerp van een onderzoek hetwelk in het kader van de Biophysische Werkgroep Utrecht-Delft werd uitgevoerd.

Bij purperbacteriën heeft men te doen met een phototaxis welke zich richt naar het intensiteitsverval van een lichtbron. Wanneer zulk een bacterie op haar weg namelijk een plaats van lagere lichtintensiteit ontmoet, dan wordt tegen een dergelijke plaats een z.g. schrikreactie uitgevoerd, als gevolg waarvan de bewegingsrichting van het organisme wordt omgekeerd.

Van dit verschijnsel werd gebruik gemaakt bij de bepaling van het werkingsspectrum van de phototaxis (= de spectrale verdeling der phototactische gevoeligheid in quantitatieve maat). In het veld van een microscoop, waarin enkele spirillen zwommen, werden twee aangrenzende lichtveldjes geprojecteerd; het licht in één dezer veldjes was zowel in intensiteit als in golflengte regelbaar. Daar de bacteriën licht van verschillende golflengten ondergaan als licht van verschillende intensiteit, kan men, door voor elke golflengte de intensiteitsverhouding van de twee velden te bepalen, waarbij de bacteriën de grens tussen de twee velden niet meer waarnemen (te zien aan het uitblijven van een schrikreactie), het z.g. werkingsspectrum der phototaxis bepalen.

Op grond van een mathematische afleiding kan men besluiten, dat het werkingsspectrum der phototaxis identiek is met het absorptiespectrum van de lichtgevoelige stof waarin het phototactische werkzame licht geabsorbeerd wordt. In tegenstelling met de sedert Engelmann en Buder heersende mening, dat de spectrale verdeling der phototactische gevoeligheid gelijk is aan het absorptiespectrum van de som van alle pigmenten in de bacteriecel, vond spreker dat dit niet geheel juist is. Het phototactisch werkzame licht bleek geabsorbeerd te worden in 1e. het bacteriochlorophyl en 2e. een of meer carotenoiden van het rhodopine en/of rhodopurpurine type. Het verrassende hierbij was, dat het in de cel zeer rijkelijk voorkomende carotenoid spirilloxanthine niet bij de perceptie van phototactisch werkzaam licht betrokken is.

Ten slotte werden nog enkele experimenten genoemd, waardoor een inzicht werd verkregen in het mechanisme van de phototaxis. Het lag voor de hand een verband te zoeken tussen de phototactische verschijnselen en de photosynthese, zulks omdat het in het pigment bacteriochlorophyl geabsorbeerde licht zowel in de photosynthese als in de phototaxis werkzaam is. Het bleek nu, dat de contrastgevoeligheid der spirillen bij stijgende lichtintensiteiten op een analoge manier afnam als dit het geval is met de verandering in photosynthesesnelheid als functie van de intensiteit (de „afgeleide" van een Blackman-kromme). Klaarblijkelijk richt de phototaxis van purperbacteriën zich naar de verandering in photosynthesesnelheid.

Hieruit volgt, dat het werkingsspectrum der phototaxis tevens de spectrale verdeling der photosynthese representeert. De conclusie moet hierbij dan getrokken worden, dat ook bij de purperbacteriën bepaalde carotenoiden bij de photosynthese zijn betrokken.

Om omstreeks 22.00 uur sloot de Voorzitter de vergadering met een woord van dank aan de beide sprekers en aan Dr Bottelier voor de genoten gastvrijheid.

VERSLAG van de Commissie tot het nazien van Rekening en Verantwoording en de bescheiden van de Penningmeester over 1948.

Ondergetekenden hebben op 5 Februari 1949 ten huize van de Penningmeester de rekening en verantwoording van 1948 en de bescheiden van de Penningmeester nagezien. Zij stellen de Ledenvergadering voor, de rekening en verantwoording van de Penningmeester goed te keuren en deze te dechargeren onder dankbetuiging voor de grote moeite en zorg, besteed aan het zorgvuldige en voorzichtige beheer van de geldmiddelen onzer Vereniging in deze financiëel moeilijke tijd.

J. L. v. Soest.
M. J. Adriani.

VERLIES EN WINST OVER 1948.

Kok-Ankersmit-Fonds

Uitgaven	*f* 2249,23	Ontvangen	*f* 2060,09
Aankoop eff.	„ 2746,02	Aflossing en koersversch.	3562,55
Saldo winst	„ 627,39		
	f 5622,64		*f* 5622,64

Brumund-Fonds.

Uitgaven	*f* 395,05	Ontvangen	*f* 875,05
Nadelig koersverschil	„ 331,81		
Saldo winst	„ 148,19		
	f 875,05		*f* 875,05

Vrije Fonds.

Nad. koersverschil	*f* 25,—	Contributies.	*f* 7876,88
Oninbare contributie	„ 600,—	Interest.	„ 204,18
Onkosten	„ 729,53	Schenking Buysman	„ 1000,—
Vergaderingen	„ 106,40		
Lidmaatschappen.	„ 315,50		
Comm. v. phytopath.	„ 48,15		
„ v. floristiek	„ 24,57		
„ v. sociologie.	„ 45,—		
„ Zuiderzee-ond.	„ 102,92		
„ v. physiologie	„ 37,60		
Herb. en bibl.	„ 1099,30		
Recueil	„ 3018,63		
Archief	„ 2488,16		
Saldo winst	„ 440,30		
	f 9081,06		*f* 9081,06

BALANS 1 JANUARI 1948.

Kok-Ankersmit-Fonds.					
Eff. en hypoth.	f 36046	24	Fonds op 1 Jan. 1948	f 36347	93
Kassaldo	„ 929	08	Saldo winst.	„ 627	39
	f 36975	32	*Fonds op 1 Jan. 1949*	f 36975	32
Brumund-Fonds.					
Effecten	f 20808	84	*Fonds op 1 Jan. 1949*	f 28387	70
Kassaldo	„ 7727	05	Saldo winst.	„ 148	19
	f 28535	89	*Fonds op 1 Jan. 1949*	f 28535	89
Vrije Fondsen.					
Effecten	f 5320	—	Fonds 100-jarig bestaan	f 2000	—
Kassaldo	„ 5775	15	Fonds Fl. Neerl.	„ 1560	80
Interest (nog te innen).	„ 108	—	Vrije fonds op		
Contrib. (nog te innen)	„ 1025	—	1 Jan. 1948 . . . f 8541,53		
Div. Debiteuren.	„ 1470	89	Saldo winst . . . „ 440,30		
Recueil (nog te innen)	„ 718	20	*Fonds op 1 Jan. 1949*	„ 8981	83
Archief (nog te innen)	„ 619	60	Crediteuren	„ 2494	21
	f 15036	84		f 15036	84

BEGROTING 1949.

Kok-Ankersmit-Fonds.			
Ontvangsten	f 1000,—	Onkosten	f 25,—
		Biol. Station	„ 250,—
		Nat. Monumenten	„ 100,—
		Herb. en Bibl.	„ 300,—
		Sigma	„ 200,—
		Wahlenbergiaterrein	„ 55,—
		Bijschrijven	„ 70,—
	f 1000,—		f 1000,—
Brumund-Fonds.			
Ontvangsten	f 800,—	Onkosten	f 25,—
		Comm. floristiek.	„ 100,—
		„ sociologie	„ 50,—
		„ wilde flora.	„ 50,—
		„ Zuiderzee-ond	„ 100,—
		Friske Gea	„ 25,—
		Herb. en Bibl.	„ 200,—
		Ivon	„ 100,—
		Bijschrijven	„ 150,—
	f 800,—		f 800,—
Vrije Fonds.			
Contributies	f 7200,—	Recueil	f 4000,—
Interest	„ 250,—	Archief	„ 4000,—
Verkoop.	„ 1000,—	Herb. en Bibl.	„ 400,—
Bijdr.	„ 1350,—	Onkosten	„ 800,—
		Vergaderingen	„ 200,—
		Contactcomm.	„ 50,—
		Comm. physiol.	„ 50,—
		„ phytop.	„ 50,—
		C.B.S. Baarn	„ 100,—
		Nat. Gen. Congres	„ 3,—
		Intern. natuurbesch.	„ 50,—
		Ned. Phytopath. Ver.	„ 10,—
		Onvoorzien	„ 87,—
	f 9800,—		f 9800,—

„Overdruk uit het Nederlandsch Kruidkundig Archief, Deel 57, 1950".

Lijst van de Leden der Koninklijke Nederlandsche Botanische Vereeniging

December 1949

BESTUUR.

Prof. Dr W. H. Arisz, *Voorzitter*	(aftr. 1951).
Prof. Dr J. Lanjouw, *Ondervoorzitter*	(aftr. 1952).
Prof. Dr J. Heimans, *1ste Secretaris*	(aftr. 1950).
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De Penningmeester der Kon. Ned. Bot. Ver.		(aftr. 1954).

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1) Gironummer der Kon. Ned. Bot. Ver. 93030, Dordrecht.

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Dr A. Scheygrond	(1937; aftr. 1953).
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A. van der Werff	(1937; aftr. 1955).
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J. Meltzer	(1946; aftr. 1964).
D. Piet	(1947; aftr. 1967).
D. Bakker	(1948; aftr. 1969).
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F. Tjallingii	(aftr. 1950).

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Dr J. Th. Henrard	(aftr. 1950).
Prof. Dr J. Lanjouw	(aftr. 1952).
Dr S. J. v. Ooststroom	(aftr. 1953).

CORRESPONDERENDE LEDEN

Dr A. F. Blakeslee (1924), Dept. of Botany, Smith College, Northampton, Massachusetts, U.S.A.

Prof. Dr O. Appel (1935), Irmgardstrasse 33, Berlin-Zehlendorff.

Prof. Dr J. Braun-Blanquet (1935), Station de Géobotanique, Chemin du Pioch de Boutonnet, Montpellier, Frankrijk.
Prof. Dr L. Buscalioni (1935), Istituto Botanico delle Universita, Bologna, Italië.
Prof. Dr A. Ernst (1935), Rigistrasse 54, Zürich.
Prof. Dr R. E. Fries (1935), Bergianska Trädgarden, Stockholm 50.
Prof. Dr N. A. Maximow (1935), Institute of Grain Husbandry, P.O. 20, Saratow, U.S.S.R.
Prof. Dr E. D. Merrill (1935), Gray Herbarium, Cambridge (Mass.), U.S.A.
Prof. Dr F. W. Oliver (1935), Departement of Botany, Egyptian University, 8 Rue Sesostris, Heliopolis near Cairo, Egypte.
Prof. Dr D. N. Prjanischnikow (1935), Iwanowskaja 23, Moskou, U.S.S.R.
Prof. Dr Reddick (1935), Department of Botany, Cornell University Agricultural College, Ithaca (N.Y.), U.S.A.
Prof. Dr J. Velenovsky (1935), Mnichowice bij Praag, Tsjechoslowakije.
Prof. Dr A. Frey—Wyssling (1948), Meilen bei Zürich.
Prof. Dr E. Gäumann (1949), Parkring 39, Zürich.

ERELEDEN.

Dr P. Jansen (1902; 1945), Amsterdam Z., Fr. van Mierisstraat 128.
Dr Ir A. W. Kloos Jr (1912; 1945), Dordrecht, Nieuwe Weg 40.
Dr A. A. Pulle (1904; 1945), Baarn, Javalaan 5.
Dr Th. Weevers (1904; 1940), Amersfoort, Bergstraat 9.

GEWONE LEDEN [1].

A. G. L. Adelbert (1938), Buitenzorg, Herbarium.
Dr M. J. Adriani (1931), Alkmaar, Papiermolenstraat 7.
E. Agsteribbe (1947), Amsterdam O., Galileiplantsoen 5 *hs*.
Dr Th. Alberda (1941), Buitenzorg, Plantk. Inst. Alg. Proefst. v. de Landbouw.
Dr L. Algera (1927), Lisse, Schoolstraat 1.
Mej. Dr G. J. H. Amshoff (1935), Utrecht, Bot. Lab. L. Nieuwstraat 106.
Mej. O. M. van Andel (1946), Groningen, N. Kijk in 't Jatstr. 50*a*.
T. H. van Andel (1946), Wageningen, Grintweg 2*a*.
Mej. Dr Ch. H. Andreas (1932), Haren (Gr.), Rijksstraatw. 330.
Tj. H. van Andel (1946), Wageningen, Grintweg 2*a*.
Mevr. S. H. Anthoni-van Helsdingen (1934), Zwolle, Ter Pelkwijkstr. 8.

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[1] Van adresveranderingen kennis geven aan de 1ste secretaris.

Dr P. M. J. T. Arens (1912), Hilversum, Blijdensteynlaan 5.
Dr W. H. Arisz (1909), Groningen, N. Kijk in 't Jatstraat 84.
Dr S. R. van Asperen de Boer (1921), Amsterdam Z., Jan van Eyckstraat 31.
Dr L. G. M. Baas Becking (1918), Nouméa, Nouvelle Calédonie.
Dr C. A. Backer (1944), Heemstede, Rembrandtlaan 13.
Dr N. P. Badenhuizen Jr (1932), Delft, Wateringsche Vest 12.
D. Bakker (1941), Ens (N.O. Polder), Enserweg 3.
Dr Ir O. Banga (1947), Inst. v. Vered. v. Tuinb. gew., Wageningen, Herenstr. 25.
Dr J. P. Bannier (1918), Wassenaar, Papegaaienlaan 15.
J. J. Barkman (1943), Leiden, Kamerlingh Onneslaan 21.
Ir J. E. Bausch (1940), Zwolle, Veerallée 33.
G. J. F. Becker (1947), Wageningen, Nude 18 .
Dr H. J. Beckers (1937), Beek (L.), Huize Nieuwenhof.
Dr W. L. Beekman (1919), Schiedam, Hoogstraat 29.
Dr J. J. Beijer (1921), Lisse, Zwanendreef 10.
Dr W. Beijerinck (1925), Biol. Station, Wijster (Dr.).
P. J. Bels (1932), Houthem-St. Gerlach, Provinciale Weg 276.
Mevr. Dr H. C. Bels-Koning (1926), Houthem-St. Gerlach, Provinciale Weg 276.
Th. Belterman (1947), Haarlem, Jordenstraat 25.
J. Bennema (1946), Loenen a.d. Vecht. Rijksstraatweg 198A.
J. Bergmans (1937), Oisterwijk (N.Br.), B 25.
Dr G. L. Bertram (1943), Aerdenhout, Vogelenzangse Weg 32.
Dr A. F. H. Besemer (1937), Wageningen, Hartense Weg 12, post Bennekom.
Dr J. G. B. Buemée (1918), Bennekom, Edese Weg 123.
Mej. A. L. van Beverwijk (1934), Baarn, Eemnesserweg 42.
A. T. J. Bianchi (1936), Bussum, Vossiuslaan 13.
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Dr Ir J. T. P. Bijhouwer (1932), Bennekom, Dennelana 3.
Dr S. Gj. Bloembergen (1930), Buitenzorg, Herbarium 's Lands Plantentuin, Java.
K. B. A. Bodlaender (1949), Utrecht, G. v. Walenborchstraat 49.
Dr K. B. Boedijn (1919), Batavia, Raden Salehlaan 45, Java.
J. E. Boeke (1944), Wageningen, Prins Hendrikweg 31.
Mevr. J. Boelaars—v. de Sman (1940), Stadionkade 34^1, Amsterdam.
A. C. Boer (1942), Zwolle, Tesselschadestraat 29.
Mej. S. de Boer (1937), Boskoop, Reyerskoop 109.
Joh. Bolman (1941), Naarden Bussum, v. d. Helstlaan 20.

Dr A. E. H. R. Boonstra (1922), Wageningen, Diedenweg 29.
Dr H. L. Booy (1937), Sassenheim, Will. Warnaarslaan 9.
H. L. Booy (1937), Scheveningen, Maastrichtsestraat 10.
J. van Borssum Waalkes (1946), Groningen, Eyssoniusstraat 21.
Mej. M. Boshuizen (1933), Oegstgeest, Juffermansstraat 21.
D. Bosschaert (1949), Utrecht, Koekoekstraat 76*bis*.
E. C. Boterenbrood (1947), Utrecht, Maliesingel 11.
Dr H. P. Bottelier (1930), Naarden, Rijksweg 31.
Mej. C. H. M. Braat (1938), Roozendaal (N-Br.), Markt 33—37.
Dr J. Brand (1916, Doesburg, Phili Gastelaarstraat 21.
Dr P. J. van Breemen (1921), 's-Gravenhage, de Bruynestraat 52.
Dr G. Bremer (1915), Wageningen, Geertjesewg 62.
Mevr. Dr D. E. Bremer-Reinders, (1932), Wageningen, Geertjesw.62
Dr R. Brink (1946), Komedieplein 1, Soerabaja.
Mej. J. M. van Brink (1942), Utrecht, Prins Hendriklaan 106 (vac. Rotterdam C., Henegouwerlaan 16*a*).
Mej. H. Brinkman (1949), Groningen, Kraneweg 25*a*.
Fop. I. Brouwer (1948), Haren (Gron.).
G. A. Brouwer (1922), Bilthoven, de Genestetlaan 32.
H. F. J. v. d. Brugge (1949), Utrecht, Brigittestraat 22.
Mevr. G. de Bruin-Brink, (1943), Utrecht, Maliebaan 127.
W. E. G. de Bruin (1945), Oosterbeek, Prins Hendrikstraat 1.
F. Brunnekreeft (1949), Utrecht, Spaarnestraat 24.
Mej. J;.G. Brunner (1943), Utrecht, J. v. Scorelstraat 17.
Mej. H. L. G. de Bruyn (1920), Wageningen, Hinkeloordseweg 5.
J. G. de Bruyn (1947), Gouderak, A 86.
Mej Dr M. P. de Bruyn Ouboter (1937), Lisse, Herenweg 347.
Mej. Dr G. E. Bunschoten (1926), Baarn, Nic Beetslaan 28.
Mej A. H. v. d. Burg (1949), Groningen, Eendrachtskade 5.
A. C. J. Burgers (1946), Utrecht, Cathrijnesingel 28*bis*.
P. D. Burggraaf (1947).
Dr Joh. H. van Burkom (1903), Apeldoorn, Jachtlaan 134.
Mevr. H. E. Casparé (1928), Rijswijk (Z.H.), Huis te Lande, van Vredenburchweg 150.
Dr J. ten Cate (1944), Amsterdam Z., Merwedeplein 15.
Dr B. J. Cholnoky (1948), Enkhuizen, Snouck van Loosen Park 17.
E. W. Clason (1926), Groningen, Lodewijkstraat 20.
Dr C. Coolhaas (1940), Wageningen, Englaan 16.
Mej. Dr I. J. le Cosquino de Bussy (1928), Amsterdam Z., Quinten Massysstraat 18 *hs*.
Dr P. J. S. Cramer (1935), Wassenaar, Koninginneweg 10.
Mej. M. C. Cremer (1943(, Lisse, Heereweg 59.
H. W. E. Croockewit (1940), Amsterdam Z., J. J. Viottastraat 27*hs*.

J. van Dalsum (1945), Middelburg, Hofplein 9.
Dr Ir H. G. Derx (1943), Directeur Treub-Laboratorium, Buitenzorg, Java.
Dr Ir W. H. Diemont (1936), Maastricht, Graaf van Waldeckstr. 41.
J. van Dijk Jr (1947), Amsterdam W., v. Hallstraat 133.
P. J. S. van Dijk (1937), Boskoop, Reijerskoop 221.
W. van Dijk (1932), Overveen, Julianalaan 66.
Dr S. J. Dijkstra (1932), Heerlen, Kloosterkoolhof 18.
Dr W. M. Docters van Leeuwen (1900), Leersum, Burgem. v. d. Boschlaan 159*a*.
C. Doets (1946), Hilversum, Diependaalse laan 286.
Dr M. A. Donk (1928), Buitenzorg, v. Limburg Stirumweg 17.
Ir J. Doorenbos (1948), Wageningen, Diedenweg 171.
Mej. A. Drijver (1947), Santpoort, Molenweg 15.
Dr E. F. Drion (1930), 's-Gravenhage, Groenhovenstr. 14.
Dr Ir J. P. Dudok van Heel (1924), Naarden, „de Rietkraag".
Ir P. R. den Dulk (1944), Den Haag, Valkenboskade 206.
P. Dullemeyer (1948), Leiden, Pieterskerkhof 40.
Mevr. H. Dutil—Voûte (1939), Makassar, p. a. Jacobson v. d. Berg & Co.
C. O. Dwars (1948), Amsterdam, Rubensstraat 82.
Dr Th. van Eek (1933), Amsterdam, p.a. Muysken, Apollolaan 193.
H. J. van Eekeren (1917), Zeist, Eikenlaan 2.
M. van Eeuwijk (1940), Velddriel, Voorstraat D. 86.
B. van Egmond (1935), Deventer, St. Jurrienstraat 8.
Mej. M. F. C. v. Egmond (1949), Utrecht, Maliebaan 100.
J. Engelen (1947), Groningen, Carolieweg 17*a*.
H. H. Evenhuis (1942), Wilhelminadorp, Lab. v. Zeelandsproeftuin.
M. L. Eversdijk (1919), Amsterdam Z., Minervalaan 12 *boven* (vac. Biezelinge).
Dr M. van Eyk (1934), Sloten (N.H.), Sloterweg 1210.
G. L. van Eyndhoven (1943), Haarlem, Eindenhoutstraat 36.
Dr F. H. Feekes (1949), Baarn, Mollerusstraat 12.
Dr Ir W. Feekes (1931), Groningen, de Ranitzplein 3*b*.
Mr Dr F. Florschütz (1920), Velp (G.), Enkweg 37.
P. A. Florschütz (1945), Utrecht, Anth. Matthaeusl. 30 *bis*.
Mej. J. Fortuyn-Drooglever (1915), Brielle, Slagveld 15.
Mevr. Dr J. Ad. Frahm-Leliveld (1926), Wageningen, Nassauweg 18.
D. Franke, Bergum (Fr.), Marktstr. 106.
R. Frantzen (1922), Rotterdam Z., Leede 22.
Dr A. J. M. Garjeanne (1899), 's-Hertogenbosch, St. Janssingel 19.
S. J. Geerts (1937), Oss, Slachthuislaan 24.
H. van Genderen (1937), Hilversum, Vaartweg 85.

Dr G. Giesberger (1931), Utrecht, Richard Wagnerlaan 22.
Dr W. A. Goddijn (1923), Leiden, Thorbeckestraat 3.
Dr M. A. J. Goedewaagen (1913), Hoogezand (Gr.), Parklaan 13.
J. Gombert (1937), Rotterdam, Crooswijkse singel 48.
J. W. Gonggrijp (1941), Amsterdam Z., Schubertstraat 37.
Dr Ir J. A. A. M. Goosens (1933), Wageningen, Rijksstraatweg 59.
Dr A. Gorter (1935), Utrecht, Nieuwe Gracht 199.
Mej. Dr C. J. Gorter (1923), Wageningen, Hamelakkerlaan 20.
G. J. M. A. Gorter (1936), Potchefstroom, Landbouwproefplaas, Transvaal.
Dr A. Grevenstuk (1940), Batavia, Boxlaan 22.
Dr K. Griffioen (1933), Buitenzorg, Pledang 25.
P. Groenhart (1934), Buitenzorg, 's Lands Plantentuin.
S. Groenhuijzen (1944), Amsterdam, Wijttenbachstraat 14^3.
A. A. de Groot (1929), Arnhem, Weverstraat 16.
Dr A. J. Haagen Smit (1932), Pasadena (Calif.), U.S.A., Institute of Technology.
Dr H. de Haan (1922), Wageningen, Prof. Ritzema Bosweg 6.
Dr Iz. de Haan (1928), Wageningen, Meidoornplantsoen 6.
A. J. M. Haans (1947), Zuilen, post Utrecht, S. van Zuylenweg 50.
Dr E. A. Hanson (1931), 8 Alma Rd., Fullerton, Adelaide, Australië.
Ir E. E. Harmsen (1946,)Boskoop, Goudse Rijweg 82.
Ir M. L. 't Hart (1942), Bennekom, Eekhoornlaan 3.
Meh. Dr A. M. Hartsema (1946), Wageningen, Dr Boeslaan 10.
Dr K. Hartsuijker (1934), Wageningen, Arboretumlaan 9.
R. J. G. M. van Hasselt (1946), Roozendaal (N.-Br.), Molenstraat 8.
H. J. v. Hattum (1947), Leiden, Volderstraat 5.
J. C. v. d. Have (1949), Groningen, Turftorenstraat 17A.
Mej. S. C. A. Haye (1947), Zeist, Utrechtse weg 10.
Mej. G. R. van Hees (1948), Amsterdam (W.), Paramaribostraat 22II.
R. Hegnauer (1949(, Leiden, Thorbeckestraat 3.
Dr J. Heimans, (1912), Amsterdam Z., Leonardostraat 10.
Ir F. Hekker (1944), Delft, Spoorsingel 99.
R. J. Helder (1942), Groningen, Gerbrand Bakkerstraat 83A.
Dr W. F. van Hell (1928), Medan (Deli), A.V.R.O.S.
Dr J. Th. Henrard (1912), Oegstgeest, Warmonderweg 54.
Dr A. W. H. van Herk (1926), Amsterdam O., v. d. Waalsstraat 37.
Dr J. W. Hes (1933), Pasoeroean, Java, Proefstation v. d. Java suikerindustrie.
J. van Hespen (1943), Wageningen, Rijnhaven 3.
Jhr W. C. van Heurn (1935), Wilp bij Deventer, F 222, Huize „Kleine Noordijk".
H. M. Heybroek (1949), Wageningen, Oude Bennekomseweg 152.

W. M. Heyl (1920), Oegstgeest, Fred. Hendriklaan 33.
Dr A. N. J. Heyn (1930), Haarlem, Wilhelminapark 13.
T. J. van Heyningen Nanninga (1927), Groningen, Paterswoldse weg 79*a*.
J. A. Hijner (1947), 's-Gravenhage, Rusthoekstraat 4.
Dr W. K. Hirschfeld (1931), Soesterberg, Amersfoortse straatweg 45.
Mej. Dr K. J. Hocke Hoogenboom (1917), Zonnemaire (Schouwen).
Mej. Dr T. Hof (1931), 's-Gravenhage, Lohengrinstraat 18.
Dr T. H. v. d. Honert (1921), Leiden, Botanisch Laboratorium, Nonnensteeg 3.
Mevr. Dr B. A. Honing-Tiddens (1927), Wageningen, Rijksstraatweg 95.
H. Hoogendoorn (1942), Oudewater, Markt B 216.
R. D. Hoogland (1943), Leiden, Witte Singel 85.
Dr J. G. ten Houten (1931), Wageningen, Bowlespark 23.
Dr A. L. Houwink (1928), Delft, Hotel Wilhelmina, Nwe Plantage.
H. J. Hueck (1945), Oss, Dr Hermanslaan 34.
H. S. C. Huijsman (1927), Doetinchem, Ds van Dijkweg 16.
B. Huisinga (1948), Utrecht, Kromme Nieuwe Gracht 28.
Dr F. W. T. Hunger (1895), Voorschoten, Veurse Weg 66.
A. M. Husson S.C.J. (1946), Leiden, St. Jacobsgracht 1.
Mej. E. J. Idenburg (1925), Utrecht, Jan v. Scorelstraat 30 *bis*.
Dr Ir G. van Iterson Jr (1909), Baarn, Eemnesserweg 89.
Mej. W. van Iterson (1938), 's-Gravenhage, Waalsdorperweg 108.
Mevr. F. A. M. Iwema-Veldhuis (1930), Amstelveen, Nieuwenhuysenlaan 2.
J. Izings (1949), Soest, Kolonieweg 6.
Mej. Dr A. Jaarsveld (1930), Amsterdam W., Overtoom 434.
Dr J. C. s'Jacob (1922), Haren (Gr.)., Dilgtweg 28.
J. A. Janse (1943), Hillegom, Loosterweg III, no 1.
Dr P. Jansen (1902), Amsterdam Z., Frans van Mierisstraat 128.
G. P. J. Jaspers (1945), Gouda, Stoofsteeg 21 (hoek Zeugestr.).
Dr S. C. J. Jochems (1918), Voorst H. 77, post Deventer.
G. J. de Joncheere (1947), Wassenaar, p.a. Jhr. W. E. v. d. Does de Bije, Groot Hoefijzerlaan 61.
B. de Jong (1942), Amsterdam O., Linnaeusparkweg 100^1.
Dr Ph. de Jongh (1935), Rotterdam, Walenburgenweg 94*b*.
Dr S. E. de Jongh (1932), Leiden, Boerhaavelaan 33.
Dr W. J. Jongmans (1900), Heerlen, Sittarderweg 61.
Dr F. P. Jonker (1932), Utrecht, Zadelstraat 19*bis*.
Mej. Dr A. Kaars Sijpesteyn (1924), Sheffield, University Hall, Endcliffe, Vale Rd. Engeland.
G. A. Kamerbeek (1938), Leiden, Vreewijkstraat 4.

Mej. A. Kamps (1948), Scheemda, Stationsstraat 35B.
Dr W. K. H. Karstens (1931), Leiden, Roodenburgerstraat 18.
Mej. Dr L. C. P. Kerling (1927), Wageningen, Lawickse Allee 7.
J. H. Kern (1937), Nijmegen, Graafse Dwarsstraat 31.
D. A. Kerpel (1936), Nijmegen, Atjehstraat 71.
H. J. Ketellapper (1949), Bilthoven, Ruysdaellaan 5.
Mej. Dr A. Kleinhoonte (1916), Delft, N. Plantage 13.
Mej. Dr c. H. Klinkenberg (1930), Wageningen, Lawickse Allée 36.
E. Kliphuis (1947), Utrecht, Prins Hendriklaan 73.
Dr Ir A. W. Kloos Jr (1912), Dordrecht, Nieuwe Weg 40.
Ir W. G. van der Kloot (1936), Den Dolder, Taveernelaan 24C.
Dr Ir A. J. Kluyver (1911), Delft, Nieuwe Laan 3.
A. Knol (1927), Baarn, Eemnesserweg 63*a*.
B. Kok (1938), Bilthoven, Beethovenlaan 10.
J. C. N. Kok (1949), Utrecht, Mauritsstraat 68.
Dr V. J. Koningsberger (1917), Utrecht, Nieuwe Gracht 187.
Mej. D. S. F. Kooijman (1945), Maastricht, St. Lambertuslaan 49.
Ir A. N. Koopmans (1926), Hengelo (Ov.), Deldenerstraat 306.
J. G. F. Korver (1935), Soerabaja, Coenboulevard 9.
Mej. Dr J. Th. Koster (1925), Oegstgeest, Warmonderweg 48.
Mevr. A. M. Koster-Bouman (1925), Gouda, Crabethstraat 73.
Dr A. J. G. H. Kostermans (1928), Buitenzorg (Java p.a. Bosbouwproefstation.
D. R. Kreger (1944), 's-Gravenhage, Annasstraat 109.
Mej. A. C. Kreulen (1915), 's-Gravenhage, Schoutenstraat 28.
Dr H. H. Kreutzer (1944), Sittard, Walramstraat 39.
Dr I. Kristensen (1949), Den Helder, Zocl. Station.
Dr G. Kruseman Jr (1927), Amsterdam Z., Jacob Obrechtstr. 16*hs*.
Dr W. M. Kruseman (1946), Deventer, Sylvanusstraat 11.
W. Kruyt (1934), Haarlem, Leeghwaterstraat 12.
Dr J. Kuijper (1905), Groningen, Troelstralaan 15.
Dr L. W. Kuilman (1928), Buitenzorg, Java, Alg. Proefstation v. d. Landbouw.
F. J. Kuiper (1938), Bilthoven, Beethovenlaan 26.
J. W. Kuiper (1947), Utrecht, Zilvergeldstr. 19.
Ch. M. A. Kuyper (1944), Amsterdam Z., Lomanstraat 63.
Dr P. A. v. d. Laan (1929), Buitenzorg, Java, Alg. Proefstation v. d. Landbouw.
Dr Ir J. H. J. van de Laar (1931), Amstenrade, Hommerterweg 43.
Mevr. Dr J. H. H. van de Laar-van der Meer (1917), Amstenrade, Hommerterweg 43.
E. Laarman (1947), Groningen, N. Kijk in 't Jatstr. 82.
J. J. Laarman (1947), 's-Gravenhage, Ampèrestraat 41.

Dr H. J. Lam (1913), Leiden, Rijksherbarium, Nonnensteeg 1.
Dr M. Hille Ris Lambers, Bussum, Middenlaan 4.
Dr J. Lanjouw (1925), Bilthoven, Hercules Seghersiaan 6.
P. Leentvaar (1946), Hilversum, Noodweg 34.
Dr W. C. de Leeuw (1926), Leiden, Roodenburgerstraat 35.
Br. Th. van Leeuwen (1948), Amsterdam, Stadhouderskade 60.
Mej. A. D. Lens (1931), Utrecht, Biltstraat 24 *bis*.
Dr A. G. M. Liernur (1921), Goirle bij Tilburg, Kleuterlaantje 4.
J. C. Lindeman (1946), Utrecht, Mariahoek 18.
W. Lindeman (1941), Amsterdam Z., Amstelkade 48 III.
Mej. B. A. Lobato (1926), Batavia C., c/o Dept. v. Ond. en Eredienst, Tjilatjapweg.
Mej. Dr J. Lodder (1932), Delft, Nieuwe Plantage 34.
J. C. Lodder (1948), Goes, D. D. van der Boutstraat 4.
W. A. Loeven (1947), 's-Gravenhage, Daguerrestraat 114.
Mej. Dr M. P. Löhnis (1915), Wageningen, Nassauweg 20.
Mej. M. Lucardie (1948), Amsterdam, Beethovenstraat 108 III.
Dr W. J. Lutjeharms (1928), Departement van Plantkunde, Universiteitscollege v. d. O. V. S. ,Bloemfontein, Z.-Afrika.
Dr R. A. Maas Geesteranus (1939), Leiden, Rijnsburgerweg 125*a*.
Mej. W. Manders (1942), Leiden, Boerhaavelaan 12.
Dr A. Manten (1939), Groningen, Florisplein 2*c*.
W. Margadant (1941), Wageningen, Oranjelaan 3.
Mevr. G. W. F. Maris Mc Arthur-Hespe (1937), Amsterdam Z., Valeriusstraat 156.
J. Marquenie (1948), Rotterdam, Sam. Mullerstraat 33A.
Dr O. P. Mechelink (1948), Oudenbosch, Markt 34.
Dr A. D. J. Meeuse (1938), 's-Gravenhage, Mispelstraat 11.
Dr B. J. D. Meeuse (1938), 's-Gravenhage, Mispelstraat 11.
J. Meltzer (1941), Bilthoven, Gezichtslaan 60.
Mej. Dr A. M. W. Mennega (1946), Utrecht, Boothstraat 10.
E. A. Mennega (1948), Utrecht, Mariahoek 18.
Mej. A. B. M. Mes (1947), Utrecht, Frans Halsstraat 61.
Mej. Dr M. G. Mes (1934), Afd. Botanie, Universiteit van Pretoria, Transvaal.
G. Meyer (1948), Utrecht, Van Lith de Jeudestraat 13.
W. Meyer (1946), Zaandam, Prins Hendrikkade 96.
Dr Ir E. Meyer Drees (1935), p.a. Hoofdkantoor Boswezen, Molenvliet West, Batavia C.
A. Middelhoek (1948), Enschede, Sweelinckstraat 34.
J. A. Miltenburg (1942), Venlo, St. Thomascollege, Hogeweg 22.
A. W. Moll (1934), Amsterdam W., Bonairestraat 15.
Dr J. C. Mooi (1935), Wageningen, Rijksstraatweg 32.

Mevr. M. B. Mooi-Bok (1935), Wageningen, Rijksstraatweg 32.
Dr M. F. Mörzer Bruyns (1938), Utrecht, Emmalaan 3.
Dr D. Mulder (1935), Wilhelminadorp, Dreef B 157.
Dr E. G. Mulder (1949), Groningen, Paterswoldseweg 89A.
F. Muller (1940), Winschoten, Engelse Laan 32.
Dr F. M. Muller (1927), Haren (Gr.), Dilgtweg 30.
J. R. Müller (1927), Heemstede, Molenlaan 3.
E. T. Nannenga (1930), Heelsum, Doorwerthse straat 4.
J. H. W. Nicolai (1945), Utrecht, Jacob van de Borchstr. 3.
Mej. Dr M. F. E. Nicolai (1929), Leiden, Roodenburgerstraat 16.
Mej. R. van Nie (1946), Groningen, Troelstralaan 32*a*.
Mevr. C. J. Niekerk-Blom (1926), Leiden, Witte Singel 30.
P. J. Nieuwdorp (1938), Leiden, Vreewijkstraat 4.
P. J. van Nieuwenhoven (1937), Maastricht, Bataviaplantsoen 7.
H. Th. Nieuwenhuijsen (1920), Utrecht, Geertebolwerk 33.
Dr Ir F. E. Nijdam l.i. (1926), Wageningen, Belmontelaan 2*a*.
L. E. Nijenhuis (1949), Woerden, Nieuwstr. 17.
R. D. Nijenhuis (1949), Woerden, Nieuwstr. 17.
J. A. Nijkamp (1941), Kijkduin, Meer en Boslaan 114.
D. Noordam (1946), Aalsmeer, Kudelstaartseweg 22.
J. Oets (1947), Amsterdam, Linnaeushof 75B.
Dr F. J. M. Offerijns (1921), Amsterdam Z., Gerrit v. d. Veenstr. 68.
E. van Olden (1932), Amsterdam Z., Leonardostr. 4 II.
Mevr. I .Olivier-Luyten (1946), Wageningen, Dr Boeslaan 14.
G. H. Oltheten (1938), Leiden, Noordeinde 37 (vac. Berkel-Rodenrijs, Rodenrijse weg 147*k*).
Dr H. C. J. Oomen (1937), Nijmegen, Vossenlaan 53.
P. G. W. J. Oordt Jr, (1949), Utrecht, Wolter Heukelslaan 50.
Dr A. J. P. Oort (1925), Wageningen, Ericalaan 5.
Mej. Dr J. Oortwijn Botjes (1930), Deventer, Zwolse weg 96.
M. L. van Oosten (1946), Wageningen, Geertjesweg 64.
Dr J. Oosterhuis (1921), Zaandam, Westzijde 241.
Dr S. J. van Oostroom (1927), Oegstgeest, Emmalaan 21.
J. D. Oppenheim (1938), c.o. E. de Jong, Bath Vam n. Tel Aviv, Israël.
Dr W. F. F. Oppenoorth Jr (1932), Delft, Roëllstraat 15.
Dr F. H. L. van Os (1945), Haren (Gr.), Westerse Drift 37.
Dr J. van Overbeek (1930), Modesta (Calif.) U.S.A., Shell Oil Comp.
Dr P. van Oye (1934), Gent, St. Lievenslaan 30, België.
Dr F. van der Paauw (1926), Groningen, Troelstralaan 21*b*.
R. Peelen (1948), Amsterdam, v. Eeghenstr. 111.
Mej. A. L. ter Pelkwijk (1940), Hoogeveen, Stationsstr. 12*c*.

Dr A. C. B. Pfältzer (1922), Twello, Hunderingen.
Dr J. W. Pfältzer (1946), Hilversum, Soestdijkerstraatweg 39.
D. Piet (1946), Amsterdam O., Kruislaan 222.
Dr L. van der Pijl (1926), Bandoeng, Huygensweg 2.
Mevr. A. J. v. d. Plaats-Niterink (1935), Utrecht, Oudegracht 411.
B. A. de Planque (1947), Utrecht, Weerdsingel W. Z., 62.
D. T. E. van der Ploeg (1940), Akkerwoude (Fr.), Kleine Laan.
Mej. Dr B. Polak (1924), Buitenzorg, Java, v. Heutzweg 2.
Dr J. W. Pont (1921), Pretoria, Bus 994, Z,-Afrika.
Mej. Dr D. J. W. Pool (1919), Groningen, Nassauplein 23*a*.
Dr L. J. Pop (1935), Rolduc, Seminarie.
Mej. A. Post (1949), Groningen, P. Campersingel 231.
Dr W. Postma (1937), Amsterdam Z., Roelof Hartplein 9*hs*.
Dr R. Prakken (1926), Wageningen, Lab. v. Erfelijkheidsonderz. der Landbouwhogeschool.
H. H. Prell (1942), Amsterdam C., Reguliersgracht 12.
Dr W. J. Prud'homme van Reine Jr (1931), Zaandam, Mauvestr.29.
Dr A. A. Pulle (1904), Utrecht, Nieuwe Gracht 187.
Dr A. Quispel (1937), Amsterdam, Corn. Drebbelstraat 25.
Dr M. H. van Raalte (1928), Buitenzorg, Daendelsweg 3.
A. Récourt (1948), Delft, v. d. Spiegelstraat 27.
H. Reedijk (1946), Gouda, Crabethstraat 45.
Th. J. Reichgelt (1938), Nijmegen, Javastraat 89.
Dr E. Reinders (1923), Wageningen, Nassauweg 5.
Mevr. R. C. Reinders—Corbach (1947), Wassenaar, Middelweg 6.
Mevr. Dr C. A. Reinders-Gouwentak (1920), Wageningen, Nassauweg 5.
Dr J. Reitsma Jr (1926), Buitenzorg, Inst. v. Plantenziekten.
Dr J. F. Reitsma (1913), Rotterdam Nolensstr. 79*a*.
Dr A. F. M. Reynders (1919), Amersfoort, Kapelweg 140.
Dr J. Rietsema (1946), Breda, Brabantlaan 6.
J. R. Rietsema (1946), Utrecht, Rembrandtkade 40.
Mej. C. J. Rijkebusch (1939), Batavia, v. Heutzboulevard 36.
A. H. G. C. Rijven (1946), Utrecht, Poortstraat 38. (vac. Venlo, Roermondse straat 63).
J. R. Roborgh (1948), Utrecht, Nieuwe Gracht, 26*bis*.
Dr P. A. Roelofsen Jr (1929), Voorburg, Beguinlaan 26.
Ir J. F. Roest (1946), Baarn, Vondellaan 4.
Dr J. W. M. Roodenburg (1919), Utrecht, van Lidth de Jeudestraat 24.
Mej. M. A. J. Rooymans (1948), Amsterdam O., Linnaeushof 66.
P. van Royen (1948), Utrecht, Zadelstraat 38*bis*.
Mej. Dr J. Ruinen (1929), Buitenzorg, 's Lands Plantentuin, Java.

Mej. A. A. de Ruiter (1947), Utrecht, Herenstraat 25.
L. de Ruiter (1946), Delft, Delfgauwse weg 190.
Dr J. D. Ruys (1918), Dedemsvaart, Huize De Rollepaal.
A. Salverda (1923), Groningen, C. H. Petersstraat 8.
R. J. Sanders, (1946), Haarlem, Lorentzplein 28.
Dr A. Scheygrond (1926), Gouda, Van Itersonlaan 7.
A. Schoenmakers (1930), Bilthoven, Nicolaïlaan 7.
G. Scholten (1949), Maarssen, Zandweg 39.
Mej. H. D. Schotsman (1942), Haren (Gr.), Rijksstraatw. 330.
A. R. Schouten (1947), Amsterdam C., Marnixstraat 290.
Mevr. H. W. van Schouwenburg-Mol (1932), Delft, Twee Molentjeskade 12.
Mej. J. C. Schreuder (1933), Groningen, Westerhavenstraat 2¹*a*.
Mej. A. van Schreven (1946), Groningen, Troelstralaan 32*b*.
Mej. Dr P. S. J. Schure (1931), Voorschoten, Leidse Weg 177.
Dr A. J. Schurink (1935), Soerabaja, Leraar Lyceum, Java.
Dr J. Schweizer (1919), Djember, Java.
G. D. M. Schwencke (1948), Voorburg, Prinses Mariannelaan 92,
Ph. N. J. W. Sedee (1948), Utrecht, Sweelinckstraat 31 *bis*.
P. Sevenster (1947), Leiden, W. Singel 61.
C. Sipkes (1917). Rockanje, Rondeweiweg 1.
Dr M. J. Sirks (1911), Groningen, Moddermanlaan 18.
Ir G. Sissingh (1939), Gorssel, Stationslaan G 245.
Jan G. Sloff (1915), Bergen op Zoom, Halsterse Weg E 84.
Dr E. van Slogteren (1912), Lisse.
Mej. W. Slooff (1934), Makassar, Inst. v. Plantenziekten.
Dr D. F. van Slooten (1933), Buitenzorg, Goaweg 88. (Java).
A. Slootweg (1947), Lisse, Hobahostraat 4.
Mej. C. M. L. Smulders (1928), Amsterdam Z., Quinten Massysstraat 18.
Mej. J. C. Sobels (1927), Utrecht, W. Heukelslaan 7.
Ir J. L. van Soest (1920), 's-Gravenhage, van Soutelandelaan 35.
Mej. A. M. H. van Someren (1944), Velp (Gld.,) Dennenweg 3.
Mej. B. G. Spierenburg (1915), Rotterdam O., Voorschoterlaan 43.
Ir A. M. Sprenger (1918), Wageningen, Lab. v, Tuinb. Plantenteelt, Haagsteeg 3.
Dr C. Spruit P. Pz. (1914), Amsterdam, Eendrachtstraat 12 I.
Dr F. A. Stafleu (1941), Proefstation voor de Java Suikerindustrie, Pasoeroean (O.-Java).
Dr G. Stahel (1914), Paramaribo, Suriname.
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REGISTER

(Namen van nieuw beschreven taxa, en nieuwe combinaties, zijn **vet** gedrukt; de inhoud van de alphabetische lijsten, aanvangende op pp. 12, 71, 116 en 347, en van de systematisch gerangschikte lijst, beginnende op p. 397 is niet in dit register verwerkt)

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Koninklijke
Nederlandsche Botanische Vereeniging

(Opgericht 15 Augustus 1845).

BESTUUR IN 1949

Prof. Dr W. H. ARISZ, *Voorzitter.*
Prof. Dr J. LANJOUW, *Ondervoorzitter.*
Prof. Dr J. HEIMANS, 1*e Secretaris.*
Mej. Dr A. JAARSVELD, 2*e Secretaresse.*
Dr Ir A. W. KLOOS Jr., *Penningmeester.*

VERSLAGEN OVER HET JAAR 1949.

JAARVERSLAG van den eersten secretaris over 1949.

Bij het opmaken van dit laatste jaarverslag aan het einde van zijn door de oorlogsomstandigheden onderbroken ambtsperiode dringt zich bij den aftredenden 1en secretaris onwillekeurig de vergelijking op met het jaarverslag van 1939.

Voor wat betreft de K.N.B.V. zijn er veel punten van overeenkomst. Zoals toen de buiten onze grenzen reeds woedende oorlog zijn schaduw over ons uitstrekte, zo speuren we thans de naweeën van het over ons heen getrokken onheil.

De reeds destijds bemoeilijkte contacten met leden en ruilconnecties in afgelegen landen zijn nog niet alle weer hersteld. De finantiële moeilijkheden met onze tijdschriften, waarover in 1939 reeds gerept werd, zijn alleen nog maar aanzienlijk verergerd. De klacht over het geringe succes met onze ingespannen en hardnekkig voortgezette bemoeiingen tot bescherming van botanisch belangrijke natuurterreinen, o.a. in Zuid Limburg, zou in dit nieuwe verslag letterlijk kunnen worden herhaald en wel naar aanleiding van nog dezelfde terreinen bij Bemelen. Zelfs ons ledental, dat in dit jaar 466 gewone leden beliep, is daarmee, na enige schommelingen tot onder 450 en tot over 500, weer op precies hetzelfde niveau gekomen als dat van 1939.

Drie leden zijn ons in 1949 door de dood ontnomen. Op 12 Juni 1949 overleed Mej. Dr LUCIE C. DOYER op 65-jarige leeftijd (geb. 10 Dec. 1883). Mej. Doyer heeft haar levenstaak gevonden aan het Proefstation voor zaadcontrôle te Wageningen, waar zij gedurende 30 jaren heeft gewerkt en zich een internationale naam op dit gebied heeft verworven. In 1938 legde zij haar kennis en ervaring neer in een handboek over zaadcontrôle tegen schimmelziekten. Mej. Doyer is sedert 1907 lid van onze vereniging geweest.

Op de jeugdige leeftijd van 25 jaren overleed op 30 Juni 1949 te Hilversum A. N. J. Wachters, biol. cand uit Utrecht. Hij was eerst sedert een jaar lid van de K.N.B.V.

De derde overledene, de Heer J. C. Harmsen, was geen gestudeerd bioloog, maar autodidact. Geboren in 1871 te St. Petersburg bracht hij het grootste deel van zijn leven in Rusland door in diverse betrekkingen; de laatste tijd voor de grote revolutie van 1917 was hij mededirecteur van een grote handelsfirma in St. Petersburg. In 1919 kwam hij met z'n gezin naar Nederland onder achterlating van alle bezittingen in Rusland. Van jongs af aan, en ook later in Nederland weer, besteedde Harmsen zijn vrije tijd aan botanische studies o.a. aan kruisings- en selectieproeven met klaver en met de Russische rubberplant *Taraxacum Kok-Sagys*. In onze vereniging was de Heer Harmsen opgenomen als lid sedert 1936.

Op de jaarvergadering nam in het bestuur Kloos voor de derde maal het penningmeesterschap op zich, en voor de derde maal uit handen van P. Jansen als voorganger.

In de commissies werden zover als dat veroorloofd is de aftredende leden herkozen en in die voor welke de statuten een verplichte roulering voorschrijven werden de door de commissies zelve voorgestelde nieuwe leden gekozen in de plaats van de aftredende.

In de loop van het verslagjaar bedankte Dr de Leeuw voor het lidmaatschap van de Zuiderzeecommissie en voor dat van de Commissie tot bescherming van de wilde flora.

Wegens vertrek van Kern naar Indonesië benoemde de ledenvergadering van 29 October den Heer W. van Dijk in de commissie van redactie van het N. Kruidk. Archief, in welke hij het secretariaat op zich nam.

De ledenvergadering van 28 Mei 1949 benoemde op voorstel van een groot aantal van onze leden Prof. Dr E. Gäumann te Zürich tot corresponderend lid.

Het bestuur kwam vier malen in bestuursvergadering bijeen, weliswaar gedurende de eerste helft van het jaar nog zonder den ondervoorzitter, die op expeditie was in Suriname. Bovendien belegde het bestuur, behalve de jaarlijkse bijeenkomst met de voorzitters en secretarissen der commissies d—i voor het vaststellen van vergaderdata voor 1950, ook een vergadering samen met de pas vernieuwde commissie van redactie voor het Recueil, ter bespreking van nieuwe financiële en technische regelingen voor de uitgave van het Recueil. Bij die gelegenheid werd de Voorzitter der Vereniging gekozen tot voorzitter van de redactiecommissie, terwijl de aftredende secretaris, ons erelid PULLE, bereid gevonden werd het secretariaat van de redactie voorlopig nog te blijven voeren.

De jaarvergadering werd gehouden op Zondag 30 Januari 49 te Utrecht met, behalve de huishoudelijke zaken, een jaarrede door WEEVERS over: „De contactcommissie voor Natuur- en Landschapsbescherming en de voorlopige Natuurbeschermingsraad.'' 's Middags spraken Dr KARSTENS over Myxomyceten en CROOCKEWIT over de woestijnflora van de Zuidelijke Staten van de U.S.A.

De zomervergadering hielden we op uitnodiging van den Heer en Mevrouw BELS in Zuid-Limburg. Op 28 Mei bezochten we in kleine groepen verdeeld het laboratorium voor de Champignoncultuur in Houthem, terwijl des middags een aantal leden onder leiding van voorzitter en secretaris van de Commissie voor de Biosociologie een prachtige wandeling maakte over de Bemelerberg en omgeving. Des avonds hielden op onze ledenvergadering de Heer en Mevr. BELS ieder een causerie, resp. over de geschiedenis van de champignoncultuur en over Problemen van de Champignonteelt. De volgende Zondag 29 Mei '49 togen we, ruim 70 man sterk, op excursie langs enkele van de mooiste gedeelten van de Belgische St. Pietersberg, onder het deskundige en vriendelijke geleide van de HH. MARÉCHAL en DARIMONT uit Luik. Ondanks de meedogenloze regen hebben alle deelnemers een prachtige indruk gekregen van de rijkdom van deze hellingen in de volle bloeitijd der orchideeën. Bij de ouderen van ons kwam daardoor de herinnering aan de geheel overeenkomstige begroeiing van de Nederlandse St. Pietersberg in z'n glorietijd wel in schrijnend contrast te staan met het besef, dat daarvan thans ook de laatste restanten geheel en voorgoed vernietigd worden.

De herfstvergadering viel op 29 October te Amsterdam met voordrachten van VAN DEN HONERT over transpiratiestroom en van LAM, die bij z'n prachtige reisfoto's vertelde van Hawai en Nieuw-Zeeland.

Zoals sedert de laatste jaren in onze vereniging gewoonte is, werden de meer gespecialiseerde voordrachten en besprekingen gehouden in door de vaste commissies belegde vergaderingen.

De commissie voor de Floristiek hield haar stereotype Paas- en Kerstbijeenkomst, die beide zeer geanimeerd waren en haar jaarlijkse excursie, naar Terhorne in Friesland.

De commissie voor Biosociologie organiseerde haar 23e en 24e sociologendag, beide in Utrecht, de eerstgenoemde op 24 April, die niet, en de andere op 20 November die wèl goed bezocht was, en verder een excursie op 28 Mei, reeds boven vermeld.

De commissie voor de Phytopathologie riep met onze leden haar contribuanten en introducés bijeen voor een vergadering op 22 October te Utrecht, gewijd aan gezwelvorming bij planten en dieren.

De commissie voor de Plantenphysiologie vergaderde zelfs drie keren: op 5 Maart, 7 Mei en 17 December; resp. te Leiden, Utrecht en Amsterdam.

De Commissie voor de Plantensystematiek en Plantengeografie kwam bijeen op Zaterdag 29 October te Amsterdam.

Voor het eerst werd dit jaar niet door ieder dezer commissies zelfstandig geconvoceerd, maar geschiedde dit centraal door de 2e secretaresse. De hiermee beoogde bezuiniging werd door verschillende tegenvallers nog niet ten volle bereikt, maar wel een aanzienlijke vereenvoudiging in de administratie. Het in gezamenlijk overleg voor een heel jaar vooruit regelen van alle vergaderdata werkt ongetwijfeld ten goede.

Ook de verzending van onze tijdschriften wordt thans centraal vanuit het 2e secretariaat geregeld, mede om onzen bibliothecaris den Heer VAN HATTUM enigszins te ontlasten. Een aantal door de oorlog verbroken ruilconnecties werd hersteld en enkele nieuwe gesloten.

De ontstellend hoge drukkosten baren den penningmeester grote zorgen. Reeds heeft het bestuur de voor overdrukken e.d. in rekening te brengen prijzen zeer aanmerkelijk verhoogd, maar nog andere en meer ingrijpende maatregelen zullen onvermijdelijk blijken.

Het eerst verschenen deeltje van de Flora Neerlandica is — voor zover het betreft de verkoop naar het buitenland — in handen gesteld van de Uitgeverij Dr JUNK. De verkoop in Nederland, ook die aan leden van de K.N.B.V. voldoet nog niet aan onze verwachtingen. Het volgende deel, dat de grassen zal brengen, bewerkt door Dr P. JANSEN is reeds ter perse en zal hopelijk spoedig verschijnen. Daarop denkt de redactie dan meteen het deel met o.a. de Cyperaceeën te laten aansluiten. Daarentegen zal van het ondertussen uitgeven van enkele gereedkomende deeltjes van de Cryptogamenflora voorlopig om finantiële redenen moeten worden afgezien.

Het bestuur heeft aan ERNST KÜSTER te Giessen, die op z'n 75ste verjaardag gehuldigd werd een gelukwens doen toekomen.

Op het 50-jarig feest van de Plantenziektenkundige Dienst werd de K.N.B.V. vertegenwoordigd door de 2e secretaresse Mej. Dr A. JAARSVELD.

De ondervoorzitter Prof. LANJOUW vertegenwoordigde ons bij het eveneens 50-jarige jubileum van het Staatsbosbeheer.

Bij de openingsplechtigheid van het Cyclotron te Amsterdam vertegenwoordigde de 1e secretaris de Vereniging.

In de adviescommissie voor de opleiding van botanische analysten werd, in de plaats van Prof. LAM, die zich terugtrok, Dr J. G. TEN HOUTEN aangewezen.

Aan de Stichting Wetenschappelijk Duinonderzoek, die tracht een biologisch station op Terschelling en op Voorne te stichten werd adhaesie bij haar streven betuigd.

Naar aanleiding van de concessieverlening tot verder afgraven van de St. Pietersberg stelden wij een request op aan den President van de Ministerraad, waarin het verlies, dat de botanische wetenschap door die afgraving lijdt, wordt gememoreerd en met klem aangedrongen op maatregelen ter beveiliging van waardevolle natuurterreinen aan de Oostelijke Maas-dalrand en daarachter gelegen in Zuid-Limburg. Van dit request zijn afdrukken gezonden aan de leden van de Staten Generaal, bestuursautoriteiten in de betrokken gebieden en aan talrijke instanties op het terrein van Natuurbescherming.

Op onze excursie van 28 Mei moesten wij bemerken, dat de mooiste orchideeënhelling van het in het hierboven bedoelde request speciaal genoemde terrein bij Bemelen als koeienweide was verpacht en in gebruik genomen. Wij hebben daarop getracht alle ter zake enigermate bevoegde autoriteiten en alle tot hulp geneigde instanties te bewegen het voor Nederland unieke en botanisch zo waardevolle terrein te redden en verder in stand te houden. Tot nu toe nog niet met geruststellend resultaat.

Op verzoek van onze Belgische collega's hebben wij naar aanleiding van de excursie van 29 Mei adhaesie betuigd bij bevoegde instanties in Brussel met de verzoeken om bescherming van de belangrijke groeiplaatsen op de Belgische St. Pietersberghellingen, welke ook bedreigd worden met exploitatie, nu niet van de kalk voor cementfabricage, maar juist van de vuurstenen.

Voorts richtten wij ons tot het Gemeentebestuur van Nijmegen in het belang van de wilde *muurbloem*, die door werkzaamheden aan de ruïne van het Valkhof dreigde verloren te gaan; hierop mochten wij een geruststellende belofte ontvangen.

Tenslotte werd onze medewerking ingeroepen bij pogingen van onze Nijmeegse leden om bescherming te verkrijgen voor enkele belangrijke terreingedeelten in het door grenscorrectie bij Nederland getrokken gebied ten O. van Nijmegen, dat reeds thans door al te grote en te handtastelijke belangstelling van Nederlandse zijde dreigt te worden ontluisterd.

Amsterdam, 31 December 1949.
De eerste Secretaris,
J. HEIMANS.

VERSLAG van de Commissie van Redactie van het Recueil des Travaux botaniques neerlandais over 1949.

In de loop van het verslagjaar verscheen de 3e aflevering van Vol. XLI waarin de volgende artikelen voorkomen:

TH. ALBERDA. The Influence of some External Factors on Growth and Phosphate Uptake of Maize Plants of Different Salt Conditions (diss. Groningen).

D. R. KREGER. An X-Ray Study of Waxy Coatings from Plants (with plates XXIII—XXVIII; diss. Delft.).

P. M. L. TAMMES. Translocation of Ferrocyanide in the Sievetubes of Palmleaflets.

F. VAN DER PAAUW. Periodische Kohlensäureassimilation von *Elodea canadensis*.

Daarmede werd het deel afgesloten; het telt in totaal 747 bladzijden.

De Commissie vergaderde op 23 September. Op deze vergadering werden de maatregelen besproken die het Bestuur had genomen ten aanzien van de nieuwe tarieven en de omvang van het volgende deel.

In de samenstelling van de Commissie kwam verandering doordat Professor VAN ITERSON als vertegenwoordiger van het laboratorium voor technische botanie te Delft vervangen werd door zijn opvolger Prof. Dr P. A. ROELOFSEN, en de heer Dr P. JANSEN als penningmeester door Dr Ir A. W. KLOOS Jr. Op verzoek van het Bestuur bleef ondergetekende zijn functie als secretaris van de Commissie tot het eind van het jaar waarnemen.

Utrecht 31 Dec. 1949.
De Secretaris der Commissie
A. A. PULLE.

VERSLAG van de Commissie van Redactie voor het Nederlandsch Kruidkundig Archief over 1949.

In het verslagjaar is deel 56 verschenen; deel 57 zal, naar met reden verwacht mag worden, in het begin van 1950 het licht zien. Het zal bevatten, naast een aantal wetenschappelijke mededelingen, de verslagen over de jaren 1946, 1947 en 1948 en de ledenlijst, bijgewerkt tot December 1949. Van deze publicaties van huishoudelijke aard zal een aantal overdrukken vervaardigd worden, bestemd voor leden die niet op ons tijdschrift geabonneerd zijn.

De secretaris der Commissie, J. H. KERN, die met grote toewijding en nauwgezetheid sedert WACHTER's overlijden deze functie heeft waargenomen en deswege op de dank der Vereniging aanspraak mag maken, vertrok in het najaar van 1949 naar Indonesië. Schrijver dezes nam zijn taak voorlopig over en werd in de ledenvergadering van 29 October tot zijn opvolger benoemd.

Overveen, 31 Dec. 1949.

De Secretaris,
W. VAN DIJK.

VERSLAG van de Commissie voor de Bibliotheek, het Herbarium en het Archief, over 1949.

Het HERBARIUM werd slechts vermeerderd met 9 planten, geschonken door de leden D. BAKKER, J. VAN BORSUM WAALKES, A. W. KLOOS en W. MEIJER. Een verzameling op alcohol van de Zuiderzeecommissie, in studie op het Hugo de Vries-laboratorium, komt in gedeelten naar de collectie in Leiden. Uitgeleend werden dit jaar 349 planten (J. ARÈNES, mej. CH. H. ANDREAS, G. KRUSEMAN), terwijl van vorige jaren nog 1906 planten uitgeleend zijn.

De BIBLIOTHEEK is 24 maal bezocht, het aantal uitleningen bedroeg 305. Aangekocht werd: P. FOURNIER, Les quatre Flores de la France (1946). Nieuwe ruilverbindingen kwamen tot stand met: Imp. Coll. Trop. Agricultures in Trinidad, Inst. Bot. Univers. Jagellonicae te Krakau en de Universiteit Marie Curie te Lublin, die periodieken uitwisselden; onder de nieuwe periodieken mogen verder genoemd worden: Brittonia (New York Bot. Garden), en Phyt. Ann. Rei Botan. (Graz). Ten geschenke werden ontvangen 166 publicaties van een aantal instituten, benevens van de volgende personen: J. J. BRAKMAN, W. BEYERINCK (4), mej. S. DE BOER, J. BOLMAN, W. VAN DIJK, P. A. FLORSCHÜTZ, G. J. M. A. GORTER, H. DE HAAN (5), J. W. HES (2), K. HÖFLER (13), A. W. KLOOS JR. (2), A. J. KLUYVER (2), W. KRUYT, W. LÜDI (2), D. MAC GILLAVRY, A. J. P. OORT, S. J. VAN OOSTSTROOM, J. VAN OVERBEEK (6), P. VAN OYE (15), L. V. D. PIJL, TH. REICHGELT, Mevr. C. A. REINDERS-GOUWENTAK (3), J. L. VAN SOEST, C. G. G. J. VAN STEENIS (3), J. E. J. VELDHUYZEN, J. VLIEGER (2), H. VAN VLOTEN (3), E. C. WASSINK (9), S. J. WELLENSIEK (3), V. WESTHOFF (7), H. ZOLLER (2).

Het ARCHIEF werd verrijkt met een geschenk van de Kon. Ver. het Indisch Instituut, door bemiddeling van het lid A. T. J. BIANCHI; het is een waardevolle correspondentie van Dr F. W. VAN EEDEN met Dr C. M. VAN DE SANDE LACOSTE over afbeeldingen van mossen in de Flora Batava.

'S-Gravenhage 5 Januari 1950.   De Secretaris,
J. L. VAN SOEST.

VERSLAG van de Commissie voor het Floristisch Onderzoek over 1949.

Ook dit jaar werden 2 druk bezochte vergaderingen gehouden in de Paas- en Kerstvacantie te Amsterdam. De voornaamste mededelingen zullen in het Ned. Kr. Archief een plaats vinden.

De zomerexcursie werd gehouden te Ter Horne onder leiding van Dr. Ir A. W. KLOOS terwijl Ir. J. VLIEGER voor de voorbereiding gezorgd had. Ofschoon het botaniseren per boot een aangename afwisseling gaf, was het slechte weer oorzaak, dat de excursie slechts 3 dagen duurde.

Voor 1950 wordt voorgesteld een excursie te houden tussen Swalmen en Susteren in de tweede helft van Juli.

Amsterdam, 31 Dec. 1949.   De Secretaris,
P. JANSEN.

VERSLAG over het jaar 1949 van de sub-Commissie voor het Zuiderzee-onderzoek.

Er kwamen in het jaar 1949 weinig gegevens over gehouden excursies binnen, mede door het feit dat in dit jaar geen vergadering van de leden werd gehouden.

Prof. Ir VAN SOEST zette zijn onderzoek van het kustgedeelte gelegen tussen Harderwijk en Elburg voort en bracht dit tot een eind.

Enige voorgenomen excursies voor het jaar 1949 zullen zo mogelijk in 1950 doorgang vinden.

Het alcohol-herbarium van de commissie, dat zich onder berusting van de Heer VAN DER WERF bevond geniet voorlopig onderdak in het Hugo de Vries-Lab. (Hortus Botanicus) te Amsterdam.

Het is de bedoeling in 1950 weer een nummer van het correspondentieblaadje te doen verschijnen.

Amsterdam, 8 Januari 1950.   De Secretaris,
H. W. E. CROOCKEWIT.

VERSLAG van de Commissie voor de Bescherming van de Wilde Flora over 1949.

Onze commissie heeft slechts weinig te rapporteren. Zij is maar heel weinig naar voren getreden in het afgelopen jaar.

Wel hebben verschillende leden in commissies en lichamen, waar zij zitting in hebben, de belangen van de botanische natuurbescherming naar vermogen behartigd, terwijl het secretariaat als gewoonlijk weer informaties heeft verschaft uit de voorhanden gegevens.

Namens onze commissie heeft de 1ste secretaris van de K.N.B.V. Prof. Dr J. HEIMANS zijn reeds lange jaren lopende pogingen om de Bemelerberg en naaste omgeving veilig te stellen, weer voortgezet.

In het begin van het jaar heeft Dr W. C. DE LEEUW bedankt als lid der commissie.

Tegen het eind van het verslagjaar kwamen wij tot de conclusie, dat de voorgenomen zandwinning onder Mook, in de pers bejubeld als een in elk opzicht toe te juichen middel, om het bedrijfsleven aan zand en de gemeente Mook aan een recreatieterrein, waar men water mag zien, te helpen, ons juist de schitterende rivierduintjes te plaatse zou kosten. Dit punt heeft in 1950 onze aandacht.

Bergen op Zoom, 31 Dec. 1949. Voor de Commissie,
JAN G. SLOFF,
Secretaris.

VERSLAG van de Commissie voor de Biosociologie en het Veenonderzoek van Nederland over het jaar 1949.

In de samenstelling van de Commissie ontstond een wijziging doordat Dr A. SCHEYGROND als lid en voorzitter vervangen werd door Dr J. HEIMANS.

Ook in dit verslagjaar organiseerde de commissie weer twee bijeenkomsten: de 23e en 24e Nederlandse Dag voor Biosociologie en Palaeobotanie, resp. op Zondag 24 April en Zondag 20 November, beide in de collegezaal van het Botanisch Laboratorium te Utrecht.

De 23e Dag was, vermoedelijk als gevolg van het buitengewoon fraaie voorjaarsweer op die Zondag, slecht bezocht. Slechts 19 leden en 9 introducé's woonden de vergadering bij. Voor de middagpauze spraken de heer J. G. DIRVEN uit Wageningen, mede namens Dr D. M. DE VRIES, over „Oecologisch Graslandonderzoek", Ir TH. A. DE BOER, eveneens uit Wageningen, over „Graslandkartering in Nederland" en de heer H. T. WATERBOLK (Groningen) over „Pollenanalytisch onderzoek bij enkele Veluwse tumuli-opgravingen". Na de middagpauze, tijdens welke de lunch gebruikt werd in het Universiteitshuis, was eerst het woord aan de heer T. VAN DER HAMMEN (Leiden) met een voordracht, getiteld „De Alleröd-oscillatie en de laat-glaciale vegetatie-ontwikkeling in Nederland" en daarna aan de heer H. J. ZWART (Leiden), die sprak over „Palynologisch veenonderzoek in West-Nederland". Dr V. WESTHOFF uit Wageningen sloot de rij van sprekers met een mededeling, getiteld „Synoecologie".

De 24e Dag was beter bezocht en werd volgens de presentielijsten bijgewoond door 33 leden en 15 introducé's. Voor de middagpauze werd het woord gevoerd door de heren D. Bakker (Ens, N.O.P.) over „De natuurlijke vegetatie van de gebieden in de omgeving van het voormalige eiland Urk" en C. VAN DEN BERGHEN uit Brussel, die sprak over „La cartographie phytosociologique en Belgique". Nadat de lunch gebruikt was in het Universiteitshuis spraken achtereenvolgens de heren W. MEIJER (Amsterdam) over „Flora en vegetatie van de Kierse Wiede, een N.W. Overijsels plassenlandschap", H. T. WATERBOLK (Groningen) over „De betekenis van het kruidenpollen voor het palynologisch onderzoek", B. A. DE PLANQUE (Utrecht) over „Palynologisch onderzoek van het holoceen en laatglaciaal (met Alleröd-schommeling) in Zuid-Oost Friesland" en M. SANDERS (Wageningen), mede namens Dr D. M. DE VRIES, over „De soortenrijkdom van graslanden in verband met de standplaats".

Ook in 1949 organiseerde de commissie op Zaterdagmiddag 28 Mei onder leiding van voorzitter en secretaris, ter gelegenheid van de zomervergadering van de K.N.B.V. een excursie, waaraan door een groot aantal leden deelgenomen werd. Gewandeld werd, onder ideale weersomstandigheden, van Houthem-St. Gerlach naar de Bemelerberg. Op de fraaie helling voor Bemelen vond de voorzitter gelegenheid te wijzen op de plantengeografische en floristische merkwaardigheden van dit schone en botanisch zo belangrijke terrein, waarna door de deelnemers hier nog lange tijd gebotaniseerd werd.

Utrecht, Dec. 1949.

De Secretaris,
Dr F. P. JONKER.

VERSLAG van de drie en twintigste Nederlandse Dag voor Biosociologie en Palaeobotanie, gehouden op Zondag 24 April 1949 in de Collegezaal van het Botanisch Laboratorium van de Rijksuniversiteit te Utrecht.

De voorzitter, Prof. Dr HEIMANS, opende des morgens om 10.30 deze, slechts door 19 leden en 9 introducé's bijgewoonde vergadering en gaf daarna het woord aan de eerste spreker, de heer J. G. DIRVEN uit Wageningen, die sprak (mede namens Dr D. M. DE VRIES) over:

Oecologisch Graslandonderzoek.

Bij het zoeken naar betrekkingen tussen de standplaats en de samenstelling van de grasmat zijn er factoren, die het niet gemakkelijk maken uit de aan- of afwezigheid van enkele plantensoorten conclusies te trekken omtrent de eigenschappen van het milieu.

De belangrijkste dezer factoren zijn:

1. de concurrentie,
2. de prioriteit,
3. de koppeling van milieu-factoren,
4. het voorkomen van ondersoorten.

Ter bestudering van de samenhang grasmat-milieu, zullen we zowel de botanische samenstelling als de milieu-factoren in cijfers moeten uitdrukken.

Botanische samenstelling.

Op ons laboratorium, dat ten dienste staat van de praktijk van de weidebouw, zijn meer of minder kwantitatieve werkwijzen in gebruik, n.l. de drooggewichtsanalytische methode en de gecombineerde $\frac{1}{4}$ dm^2-frequentie- en rangorde-methode.

Bij de drooggewichtsanalytische methode wordt de gewichtsverhouding bepaald in een verzamelmonster, bestaande uit een groot aantal grepen gras of boorsels (bij een kort gewas). Tengevolge van seizoens- en weersinvloeden zijn deze gewichtspercentages aan sterke schommelingen onderhevig.

Minder afhankelijk van de tijd van bemonstering zijn de resultaten verkregen met de gecombineerde $\frac{1}{4}$ dm^2-frequentie- en rangordemethode. Hierbij worden de plukjes of boorsels afzonderlijk bekeken, waarna voor elke soort bepaald wordt, in hoeveel per honderd plukjes deze voorkomt en in hoeveel ze domineert, eventueel de 2e, 3e, enz. plaats inneemt. Vanwege haar geringere variabiliteit in verband met de tijd van monsterneming leent zij zich uiteraard voor de typering van grasland.

Bij ons type-onderzoek, dat gecombineerd wordt met grondmonsteronderzoek, wordt de botanische samenstelling volgens beide methoden onderzocht. Hierdoor verkrijgen we gegevens ter bestudering van de oecologie van:

1. de afzonderlijke graslandplanten,
2. de associaties,
3. de typen,

4. de enkelvoudige gezelschappen of societates,
5. de landbouwkundige groepen der graslandbestanddelen,
6. de hoedanigheidsgraad.

De milieufactoren.

Het complex milieu-factoren kunnen we doen uiteenvallen in de volgende hoofdgroepen:

1. Klimatogene — Perioden van strenge vorst en droogte kunnen tijdelijk sterke verschuivingen in de botanische samenstelling veroorzaken.
2. Edaphische — De vochtigheidstoestand wordt in het veld bepaald, terwijl we de overige gegevens verkrijgen uit het grondmonster- en profielonderzoek.
3. Biotische — Onder deze is de invloed van de mens wel het belangrijkste. Voor een deel wordt zijn invloed in de edaphische factoren uitgedrukt. De gebruikswijze van het grasland staat echter op zichzelf.

Verband botanische samenstelling en standplaats-factoren.

Aan de hand van lantaarnplaatjes werden enkele van de gevonden resultaten vertoond en toegelicht.

Hieruit blijkt, dat we bij verwerking volgens één milieu-factor vaak een schijnverband vinden. Dit is een gevolg van het gekoppeld voorkomen van milieu-factoren, zodat we niet direct weten, welke van de standplaatsfactoren voor de aard van de plantengroei van de grootste betekenis is. Door toepassing van een polyfactor-analyse zal men het verband van de botanische samenstelling en de milieufactoren beter kunnen opsporen. Hiervoor is echter het materiaal nog niet groot genoeg.

Het oecologische graslandonderzoek is thans in een zodanig stadium gekomen, dat we aan de hand van de botanische samenstelling aanwijzingen kunnen geven omtrent de eigenschappen van de standplaats.

De tweede spreker was Ir Th. A. de Boer, eveneens uit Wageningen; zijn voordracht was getiteld:

Graslandkartering in Nederland.

Het is voor de landbouwwetenschap en -voorlichting van groot belang een methode te kennen, waarmede men in het veld tot een waardebepaling van het grasland kan komen.

Door D. M. de Vries c.s. is veel omtrent de oecologie van graslandplanten vastgelegd. Verder is uit de practijk en proefnemingen één en ander bekend omtrent de kwaliteit der graslandplanten. Eveneens zijn door genoemde auteur methoden uitgewerkt om de botanische samenstelling te typeren en in cijfers vast te leggen. Uit onderzoekingen van M. L. 'T HART zijn we nader ingelicht omtrent het opbrengstniveau van ons grasland.

Ons ideaal is nu om door combinatie van deze, in verhouding tot de complexheid van de milieufactoren, schaarse gegevens te komen tot een waardebepaling in het veld van een afzonderlijk graslandperceel. Wij twijfelen er niet aan, dat het wel altijd tot een benadering van dit ideaal zal blijven.

De moeilijkheid is n.l. dat door genoemde onderzoekers vaak wel een regressie tussen de verschillende waardebepalende elementen en milieufactoren is gevonden, maar dat door de complexheid van het object en het milieu geen nauwkeurig verband te bepalen is. Een moeilijkheid aan alle veldbiologische vraagstukken eigen.

Een voordeel van ons taxatiewerk is, dat we het object van eigen aanschouwing kennen en niet als abstractie van een aantal cijfers. Hiermede wordt echter de subjectiviteit in het onderzoek gehaald. Nu trachten we door *een analyse van de taxatie* het gevaar hiervan zo klein mogelijk te maken. Toch zullen steeds bij ons onderzoek de ervaring en het inzicht belangrijke elementen blijven.

In het veld worden, al naar gelang van de vereiste nauwkeurigheid, de volgende bepalingen gedaan: een soortenlijst, een schatting in gewichtspercentages der landbouwkundige groepen, een berekening der hoedanigheidsgraad (Hg) met behulp van de gemiddelde waarderingscijfers dezer geschatte groepen, de zodebezetting, aangeven van het type aan de hand van de hoogfrequente typevormende soorten, afzonderlijke schatting van het gewichtsaandeel van veel voorkomende onkruidsoorten, de overheersende plantensoort.

Daarnaast worden gegevens omtrent het bodemprofiel verzameld; dit gebeurt meestal in samenwerking met de Stichting voor Bodemkunde of de Cultuurtechnische Dienst.

De belangrijkste botanische gegevens, die we op deze wijze kunnen verkrijgen, zijn het zgn. *waarderingsgetal* (product van Hg en zodebezetting) en het *type*. Het eerste zegt ons iets omtrent de kwaliteit van het gewas en, bij voldoende gegevens omtrent bodemprofiel en waterstand, iets omtrent de opbrengstmogelijkheden. Het type kan ons inlichten omtrent de meer potentiele waarden van het milieu.

De hoedanigheidsgraden en de waarderingsgetallen worden in 6 klassen ingedeeld en met kleuren in kaart gebracht. De typen worden door combinatie van lijnarceringen, open en gesloten figuurtjes in kaart gebracht.

Op deze wijze zijn karteringen verricht of in bewerking o.a. van het ruilverkavelingsgebied te Staphorst, in verband met verbeteringsmogelijkheden; van een aantal bedrijven op het Kampereiland, waar door middel van de oppervlakten der percelen kwaliteitscijfers voor de bedrijven worden berekend; in het randgebied van de N.O.P. om de invloed van verdroging op de botanische kwaliteit van het grasland na te gaan; in Z.W. Friesland op kostprijsberekeningsbedrijven, om het verband met de kostprijs van de melk na te gaan.

Daarnaast worden in samenwerking met de Cultuurtechnische Dienst bepalingen gedaan van vegetatievakken, die, rekening houdende met de structuur van het betrokken gebied, uitgezocht zijn. Hiervan worden zoveel mogelijk milieufactoren verzameld, zodat men tot grafische verwerking kan overgaan. Op deze wijze hopen we onze oecologische kennis nog uit te breiden.

Vervolgens sprak de heer H. Tj. Waterbolk (Groningen) over:

Pollenanalytisch Onderzoek bij enkele Veluwse tumuli-opgravingen.

In 1947 en 1948 werd door de Rijksdienst voor het Oudheidkundig Bodemonderzoek een aantal grafheuvels opgegraven op de Veluwe, o.a. bij Schaarsbergen, Ugchelen en Putten. Grondmonsters van de ondergrond werden pollenanalytisch onderzocht met het doel na te gaan, hoe de plantengroei tijdens de bewoning was en welke veranderingen er plaats vonden tussen het tijdstip van aanleg van verschillende tumuli in een zelfde gebied. Ondanks soms zeer slechte conservatietoestand konden toch steeds binnen redelijke tijd 150 boompollenkorrels worden geteld.

De door van Giffen op grond van de aanwezigheid van heidepodsolprofielen onder grafheuvels en door Florschütz en Wassink op grond van pollenanalytisch veenonderzoek verkregen conclusies betreffende de heideuitbreiding bij het begin van het Bronzen tijdperk (ca. 1500 v. Chr.) konden worden bevestigd. Neolithische grafheuvels bij Putten, Schaarsbergen (2 ×) en Ugchelen bevatten in de ondergrond resp. 6, 5, 9 en 20 % *Ericaceae*, terwijl vier grafheuvels bij Schaarsbergen en een bij Ugchelen uit de Bronstijd resp. 50, 59, 78, 79 en 47 % opleverden. Bij een groot aantal Drentse grafheuvels werd een overeenkomstig resultaat verkregen. Alleen laatneolithische en aeneolithische tumuli gaven soms percentages *Ericaceae*, welke die van vroege bronstijdtumuli benaderden. Late bronstijd- en ijzertijdheuvels bevatten evenwel meer heidestuifmeel, nl. resp. ongeveer 200 en 300 %. Oppervlaktemonsters uit recente tijd leveren 1000—4000 % op!

Uit een en ander blijkt, dat sinds het Neolithicum de uitbreiding van de heide min of meer geleidelijk heeft plaats gevonden. Van een hoogpresente begeleider in het Eiken-Berkenbos werd *Calluna* tot dominante soort over grote uitgestrektheden.

Voorts waren belangwekkend de gevonden percentages van de linde. Bij alle neolithische heuvels waren deze opvallend hoog: resp. 18, 34, 54 en 22 %, terwijl de ondergrond van de bronstijdheuvels lagere, maar toch nog belangrijke hoeveelheden bevatten: resp. 14, 26, 10, 22 en 13 %.

In Brabant werden nog geen neolithische tumuli onderzocht, wel enkele uit de bronstijd. Daarbij werden waarden gevonden, die vaak nog iets hoger waren, dan die van synchrone Veluwse tumuli. Geen enkele Drentse grafheuvel uit de bronstijd of later bevatte waarden, hoger dan 1 of 2 %, terwijl van neolithische grafheuvels slechts enkele zo hoge percentages bevatten, dat op grond daarvan tot voorkomen van de linde kon worden geconcludeerd. Bij het stuifmeel onderzoek van een grafheuvelcomplex bij Zeijen werden gegevens verkregen welke er op wijzen, dat de linde hier reeds in het laatst van het Neolithicum was verdwenen.

Het blijkt wel, dat er in voorhistorische tijd een voor de linde belangrijke klimaatgrens door ons land schoof, welke vooral duidelijk was bij het begin van het bronzen tijdperk, toen de boom in Drente volledig ontbrak, op de Veluwe en in Brabant echter nog volop aanwezig was. Afgezien van deze geografische verschillen blijkt er een algemene achteruitgang van de linde waar te nemen, welke reeds in het Neolithicum aanvangt, en, zoals aanstonds nog nader zal worden uiteengezet, bij de aanvang van het Subatlanticum eindigt met een volledig uitsterven, niet alleen in ons land, maar over grote gebieden van N.W. Europa. Gezien het huidige zuidelijke verspreidingsgebied van deze boom ligt het voor de hand deze achteruitgang te wijten aan de algemene achteruitgang van het klimaat na het mesolithische postglaciale warmteoptimum.

Dat de linde bij de aanvang van het Subatlanticum overal is verdwenen blijkt uit de veendiagrammen: boven de grenshorizon treedt slechts uiterst sporadisch *Tilia*stuifmeel op. Hoewel de onder de grenshorizon gevonden waarden steeds veel lager zijn, dan die onder grafheuvels, is de algemene tendens, zowel wat de geografische als de chronologische en absolute verschillen betreft, overeenkomstig. Men vergelijke het diagram van Sourbrodt (Hautes Fagnes) van Florschütz met dat van Roswinkel (Florschütz & Wassink). In het eerste relatief hoge waarden, welke tot in de grenshorizon doorlopen, in het laatste zeer lage, welke op het niveau van de bekende bronsvondst (vroege bronstijd) reeds tot 0 gedaald zijn. De diagrammen van Eshuis van de Peel zijn typisch intermediair.

Hoe uiterlijk en verdere samenstelling van het Atlantische lindenbos zijn geweest, is vooreerst nog niet duidelijk. Wellicht mag men denken aan het enige natuurlijke lindenbos in W. Europa, dat van het Alpenvoorland (Trepp). Dit gezelschap vervangt aldaar lokaal het overigens op soortgelijke grondsoort voorkomende Eiken-Haagbeukenbos als climax. Het Veluwse lindenbos zal men dan ook vooral moeten zoeken op die gronden, die thans het Eiken-Haagbeukenbos zouden dragen. Dat deze gronden vroeger veel groter uitgestrektheid innamen dan men thans zou denken is waarschijnlijk; vele oorspronkelijke Eiken-Haagbeukenbosgronden zijn dermate gedegradeerd, dat ze thans tot het paraclimaxcomplex van het Eiken-Berkenbos behorende vegetaties dragen (Westhoff).

Het is duidelijk, dat het bovenstaande een belangrijk argument is tegen het samennemen van eik, iep en linde in de diagrammen tot het „Quercetum mixtum". Nu het totaal verschillende gedrag van deze bomen blijkt, dient dit begrip, dat bovendien elke plantensociologische basis mist, overboord geworpen te worden.

Bij het onderzoek van de grafheuvels werden verder nog gegevens verkregen betreffende de kruidenflora in Neolithicum en Bronstijd. Zo werd onder een neolithische heuvel korenstuifmeel gevonden en tevens veel pollen van *Plantago lanceolata*, een plant, waarvan de opkomst volgens Iversen samen gaat met de eerste landbouw in het Neolithicum.

De vierde spreker was de heer T. van der Hammen uit Leiden. Hij sprak over:

De Alleröd-oscillatie en de laat-glaciale vegetatie-ontwikkeling in Nederland.

Onze huidige kennis van de flora van het Laat-glaciaal in Nederland hebben we voor het belangrijkste deel te danken aan Florschütz. Aan de hand van door hem uitgevoerde onderzoekingen van laatglaciale venen en moeraskalkafzettingen, kon hij het algemene verloop der vegetatieontwikkeling vaststellen: van toendra via parklandschap naar subarctische bossen.

In 1901 toonden Hartz en Milthers in Denemarken een tijdelijke klimaatsverbetering aan, die zij Alleröd-oscillatie noemden, voorafgegaan en gevolgd resp. door de Oudere en de Jongere *Dryas*-tijd.

Sindsdien is deze klimaatsschommeling door verschillende auteurs in andere landen aangetoond. In Nederland was het FLORSCHÜTZ die in 1939 voor 't eerst de mogelijkheid naar voren bracht van het voorkomen van afzettingen uit de Alleröd-tijd bij Wiene.

Door recente onderzoekingen van enkele palynologen over de morphologie van stuifmeelkorrels is het mogelijk geworden reeds een betrekkelijk groot aantal soorten kruidenpollen zeker te determineren. Hiermede hebben wij een belangrijk middel gekregen tot dieper-gaand floristisch onderzoek van het Laatglaciaal, daar afzettingen uit deze tijd immers vaak rijk zijn aan kruidenpollen.

IVERSEN heeft voor 't Laatglaciaal een nieuw type van diagram ontworpen, waardoor de vegetatieontwikkeling, onder omstandigheden waarbij behalve de bossamenstelling ook de bosdichtheid aan veranderingen onderhevig is, duidelijker weergegeven wordt. Als basis van procentberekening neemt hij de som van de pollenkorrels van de voornaamste windbloeiende planten, zowel bomen, struiken als kruiden. Voor onze diagrammen gebruikten we deze voorstellingswijze van IVERSEN.

Door pollenanalytisch onderzoek van een gyttja-afzetting uit 't Hykermeer in Drente konden wij de Allerödoscillatie in Nederland aantonen. Tevens bleek daarbij de vergaande overeenkomst in de kruidenflora van het Laat-glaciaal in Nederland met die van Denemarken in dezelfde tijd. *Helianthemum* en *Hippophaë* komen hoofdzakelijk alleen in de Oudere *Dryas*-tijd voor, *Empetrum* daarentegen heeft z'n grootste uitbreiding in de Jongere *Dryas*-tijd. Opvallend is verder het voorkomen van *Artemisia*. *Artemisia* wordt, samen met o.a. *Hippophaë* en *Helianthemum*, wel gerekend tot de z.g. „steppe-elementen" in de laat-glaciale flora; zij zouden dus op een droog klimaat wijzen. *Juniperus* moet zeer algemeen geweest zijn in laat-glaciale tijd, gezien de vrij hoge pollenpercentages.

Sinds de bewerking van 't materiaal van 't Hykermeer konden wij op vier andere plaatsen in Nederland de Alleröd-oscillatie pollenanalytisch aantonen. Drie van de hierbij samengestelde diagrammen zijn van plaatsen in het Zuiden en Oosten van ons land; hierover kunnen we nog geen nadere mededelingen doen, daar de bewerking van dit materiaal in verband met andere onderzoekingen uitgevoerd is. Voorts is er een diagram van Den Treek (Utrecht). Het laatglaciale veen van Den Treek is een „Alleröd-laag". Zowel in de Jongere als in de Oudere *Dryas*-tijd heeft hier stuiving plaats gehad. Het blijkt dat het „dekzand" op deze plaats in de Jongere *Dryas*-tijd moet zijn afgezet, in tegenstelling b.v. met dat bij Hengelo (FLORSCHÜTZ, 1939), waar onder het dekzand reeds 20 % *Corylus* aanwezig is, en de stuiving dus in het Praeboreaal optrad.

Daarna sprak de heer H. J. Zwart, ook uit Leiden, over:

Palynologisch veenonderzoek in West Nederland.

Volgens de geologische kaart zijn in West-Nederland twee soorten veen te onderscheiden, het laagveen en het moerasveen. Het eerste is het grote oppervlakteveen, het tweede het tussen de oude duinen gelegen veen. Alleen enkele diagrammen van het oppervlakteveen zullen hier behandeld worden.

Practisch alle kwartaire afzettingen in West-Nederland zijn te beschouwen als ontstaan door een steeds wisselend spel van trans- en regressies van de zee. Zo is het grote Hollandse veen gegroeid nadat door een regressie aan het eind van het atlanticum een groot gebied droogviel. Dit veen is dus van subboreale en subatlantische ouderdom.

Tot dusver is dit veen alleen onderzocht door Polak en Vermeer-Louman, waarvan de laatste een diagram uit de Riekerpolder gepubliceerd heeft. Wij zullen hier een drietal diagrammen van Uitgeest en een uit Voorschoten bespreken. Hierbij zijn een tweetal zaken van belang, n.l. ten eerste de bosgeschiedenis en ten tweede de vegetatieontwikkeling. Een goede indeling van het subboreaal en het subatlanticum bestaat er nog niet. Een van de redenen hiervan is, dat practisch alle bomen reeds hun belangrijkste uitbreiding gehad hebben. Alleen de Beuk en de Haagbeuk zijn nog in opkomst. Het is echter gebleken, dat ook de Hazelaar in het pollendiagram aanwijzingen kan geven. De curven van deze struik blijken namelijk in het geheel niet parallel te lopen met die van het *Quercetum mixtum*, zoals Vermeer-Louman vond. Aan het begin van het subboreaal blijkt de *Corylus*lijn meestal vrij snel te stijgen, maar gaat nooit hoger dan 70 %. Tijdens het subboreaal zijn er enkele schommelingen maar op de grens met het subatlanticum is er een duidelijke top. Terwijl iets hoger Beuk en Haagbeuk hun maximale uitbreiding hebben, blijkt in de *Corylus*lijn wederom een top aanwezig te zijn. Op deze manier zou het mogelijk zijn de grens atlanticum-subboreaal en subboreaal-subatlanticum in een pollendiagram vast te leggen. De overige bomen blijken teveel aan locale omstandigheden gebonden te zijn, dan dat zij enige aanwijzing zouden verschaffen. De grens subboreaal-subatlanticum, die gekenmerkt is door de overspoeling met jonge zeeklei op enige plaatsen, blijkt in het diagram geheel overeen te komen met de „grenshorizon" van Vermeer-Louman. Opvallend is, dat de dikte van het tijdens het subboreaal gevormde veen zeer constant is en in alle vijf diagrammen 1,40 m bedraagt.

Voor de tijd van —1500 tot —300, dat is ongeveer de duur van het subboreaal geeft dit een groei van 1 mm per jaar. De maximale *Fagus*uitbreiding valt dan ongeveer in 300 na C., hetgeen samenvalt met de eerste belangrijke uitbreiding van de gecultiveerde granen. Opvallend is het hoge *Pinus*-percentage in het kleiïge veen op de drooggelopen zeeklei. Een afdoende verklaring hiervoor is niet gevonden.

De vegetatieontwikkeling werd bestudeerd door het kruidenpollen ook te tellen. Steeds bleek de successie te beginnen met een zoutflora, gekenmerkt door het hoge *Chenopodiaceeën* en *Alsineeën* gehalte. Vervolgens meest een Riet-Zeggenstadium, daarna een Moerasvarenvegetatie om dan òf de *Sphagnetum*kant òf de *Quercetum*kant op te gaan.

De ontwikkeling werd meestal afgebroken door een nieuwe overstroming van de zee, waardoor de cyclus, te beginnen met de zoutplantenvegetatie, weer kon beginnen.

Dr V. WESTHOFF uit Wageningen sloot de rij van sprekers met een mededeling, getiteld *Synoecologie*. Van deze voordracht werd geen samenvatting ontvangen.

De voorzitter sloot hierna deze vergadering.

VERSLAG van de vier en twintigste Nederlandse Dag voor Biosociologie en Palaeobotanie, gehouden op Zondag 20 November 1949 in de Collegezaal van het Botanisch Laboratorium te Utrecht.

Deze vergadering werd bezocht door 33 leden en 15 introducé's. Nadat de voorzitter, Prof. Dr J. HEIMANS met een woord van welkom de bijeenkomst geopend had, gaf hij het woord aan de eerste spreker, de heer D. BAKKER (Ens, N.O.P.), die sprak over:

De natuurlijke vegetatie van de gebieden in de omgeving van het voormalige eiland Urk.

In 1941, na het sluiten van de dijk in 1940, werd een begin gemaakt met het droogmaken van de Noordoostpolder. Het Westen van deze polder, waarvan het laagste gedeelte 4.40 m beneden N.A.P. ligt, viel eerst in 1942 droog. In 1941 was het land in de omgeving van Urk reeds boven water gekomen, daar dit niet meer dan 0.50 tot 1.50 m beneden N.A.P. ligt. De grindrijke uitloper van het eiland Urk, bekend als „De Staart", ligt zelfs boven N.A.P. en steekt dan ook duidelijk in het omringende landschap af. Het lage, moerassige westelijke gedeelte van de polder, dat sinds kort ontgonnen is, werd al spoedig door een soortenarme, dichte riet- en biezenvegetatie ingenomen. De gebieden in de omgeving van Urk bleven daarentegen tot nu toe ijl begroeid. Door de hoge ligging en de veelal lichte grondsoort zijn deze gebieden in het voorjaar en de zomer zeer droog, waardoor kieming en vegetatieve uitbreiding van vele plantensoorten bemoeilijkt wordt.

De bodemgesteldheid van dit land bij Urk, dat ongeveer 800 ha groot is, loopt sterk uitéén. De volgende gebieden met een min of meer homogene bodemgesteldheid kan men onderscheiden, waarbij men dan bedenken moet dat de verdeling in werkelijkheid zeer grillig en bont is: 1) Het keileemgebied, al of niet bedekt met grof zand. 2) Een veencomplex, met plaatselijk een pH tussen 3 en 4. In dit veen lopen met zand en klei opgevulde sloten, die vermoedelijk in de Middeleeuwen gegraven zijn. 3) Een afzetting van zure kwelderklei, meestal bedekt door een laagje zand.4) Grofzandige afzettingen, het z.g. Urk-zand. 5) Zandige stortgronden, die bij de inpoldering daar gebracht zijn. 6) De grindrijke „Staart" van Urk.

Hoewel de begroeiing nog steeds ijl is, bedraagt het aantal soorten hogere planten toch reeds 168. Er werden 9 verschillende bladmossen en 3 korstmossoorten gevonden. Van deze 168 soorten hogere planten treden er 62 sterk op de voorgrond. Van deze 62 algemene soorten zijn er 25 uitgesproken windverspreiders. Er komen 14 halophyten voor en meer dan de helft van het aantal soorten werd niet voor de droogmaking op Urk gevonden. *Bryum bicolor* is een zeer algemeen mos in dit gebied.

Tot 1947 werd het *Puccinellieto distantis-Spergularietum salinae* als de dominerende associatie van dit gebied opgegeven, terwijl op de droogste zandgronden vrijwel alleen mosgroei mogelijk was. De laatste drie jaren is hier verandering in gekomen, hoewel de bovengenoemde begroeiing nog zeer veel voorkomt. Op de kwelderklei en de vochtige plekken in het veen- en zandgebied is riet langs vegetatieve weg uit het lage gedeelte van de polder binnengedrongen. Het milieu was hier wel geschikt voor een lichte rietvegetatie, echter niet vochtig genoeg voor de kieming van rietzaad. Vooral op de kwelderklei is dit duidelijk. *Cirsium arvense* en *Tussilago Farfara* konden zich onder deze lichte rietbegroeiing op de kwelderklei door middel van zaad vestigen. Kwelderklei tekent zich thans door zijn welige vegetatie duidelijk in het landschap af. De grens is dikwijls aan de vegetatie haarscherp waar te nemen.

Op de zandgronden zijn degeneratiestadia van het *Puccinellieto distantis — Spergularietum salinae* algemeen. Soorten als *Echinochloa Crus-galli*, *Polygonum aviculare* en *Trifolium repens* dringen in grote getale deze associatie binnen.

Op de in de zomer zeer droge zandgronden kunnen *Gnaphalium luteo-album*, *Erigeron canadensis* en soms ook *Crepis tectorum* facies-vormend optreden.

Op zilte plaatsen komen het *Salicornieto-Spartinetum*, het *Puccinellieto distantis-Spergularietum salinae* en het *Armerion maritimae* in min of meer zuivere vorm voor.

Het veengebied is op de zuurste plekken onbegroeid. Ligt de pH ongeveer bij 5, dan is dikwijls een facies van *Holcus lanatus* aanwezig. Vochtige, weinig zure veenplekken hebben een ijle rietbegroeiing. Wanneer er een dun laagje zand op het zure veen ligt, dan treedt er een facies van *Juncus bufonius* op. De dichtgespoelde sloten zijn met riet begroeid.

De vegetatie op het keileem is over het algemeen nog ijl. De laagste plekken hebben een lichte rietbegroeiing. Op de hogere gedeelten zijn naast bladmossen, *Epilobium* spec., *Taraxacum* spec., *Erigeron canadensis* en *Trifolium repens* de dominante soorten.

De „Staart" van Urk wordt gekenmerkt door *Sedum acre* en *Bryum* spec.

De tweede spreker was onze buitenlandse gast, de heer C. VANDEN BERGHEN uit Brussel, die sprak over:

La Cartographie phytosociologique en Belgique.

Sous l'égide de l'*Institut pour le Développement de la Recherche scientifique dans l'Industrie et l'Agriculture* (I.R.S.I.A.), créé immédiatement après la dernière guerre, fonctionne, en Belgique, un *Comité de la Carte pédologique et phytosociologique* dont le président est Mr V. VAN STRAELEN. Trois centres de cartographie pédologique sont, actuellement, en activité (Gand, Louvain, Gembloux). Un centre de cartographie phytosociologique, sous la direction de MM J. LEBRUN et A. NOIRFALISE, fonctionne depuis 1948.

Les principes phytosociologiques suivis par les collaborateurs aux travaux de la carte sont ceux de l'école franco-suisse (BRAUN-BLANQUET). Sur le terrain, les cartes cadastrales au 1/2.500e ou au 1/5.000e sont utilisées. La minute de chaque planchette est dessinée au 1/10.000e. Elle sera publiée à l'échelle du 1/20.000e. Quatre planchettes (Plateau des Tailles, en Ardenne, et région gantoise) sont actuellement achevées. Une notice accompagnera chaque planchette.

Fréquemment des contacts s'établissent entre pédologues et phytosociologues. Les résultats de cette collaboration sont excellents.

Grâce aux travaux de la cartographie, notre connaissance de la végétation de notre pays a fait de sérieux progrès. Mr A. NOIRFALISE a pu étudier la composition floristique et la synécologie des hêtraies ardennaises. Personnellement, nous nous sommes intéressés aux tourbières de l'Ardenne orientale. Les groupements végétaux qu'on y observe présentent un caractère nettement atlantique: jonçaies à sphaignes, tourbières de pente à *Narthecium ossifragum*, lande à *Erica tetralix*.

La cartographie phytosociologique a déjà rendu des services d'ordre économique. Nous avons, notamment, pu déconseiller la plantation d'épicéas dans les landes à *Calluna* et *Scirpus caespitosus* (forme ardennaise de *l'Ericetum tetralicis*) du Plateau des Tailles.

Na de lunch sprak eerst de heer W. MEIJER (Amsterdam) over:

Flora en vegetatie van de Kierse Wiede.

De Kierse Wiede is een typisch N.W. Overijssels veenplassengebied gelegen op de overgang van veen naar zandgrond, tussen Wanneperveen en Meppel. Het landschap wordt hier gevormd door plasjes met *Nymphaea*, *Schoenoplectus lacustris* en *Stratiotes*-vegetaties, die door verlanding in *Cicuta*-drijftillen overgaan, door uitgestrekte *Equisetum limosum*begroeiingen, moerasweiden met veel *Carex diandra*, *Dactylorchis incarnata*, *Liparis Loeselii*, *Parnassia palustris* en *Calamagrostis neglecta.*

Het geheel wordt a.h.w. geflankeerd door een grote Eendenkooi en een typisch *Alnus*moeraswoud met o.a. *Impatiens Noli-tangere* in de ondergroei. Bryologisch zijn vooral de *Carex diandra*weiden interessant doordat ze de typische combinatie van *Scorpidium scorpidioides*, *Fissidens adiantoides*, *Campylium stellatum*, *Riccardia pinguis* e.a. vertonen en doordat *Sphagnum teres* er vaak de verdere verzuring inluidt die naar *Sphagneta* met *Vaccinium oxycoccus* en *Erica Tetralix* uitloopt; opvallend is in dit gebied dat met kwel van ijzerhoudend water in de Z.O.hoek het sterke domineren van *Equisetum limosum* gepaard gaat.

Over de *methode* van onderzoek zij vermeld dat daarbij niet gestreefd werd naar het vaststellen van associaties in de zin van de Fr.-Zwitserse school in de plantensociologie.

Associaties, gedefinieerd als plantengezelschappen van constante floristische samenstelling, gekenmerkt door kensoorten en constante begeleiders (zie WESTHOFF, „Inleiding in de plantensociologie”) zijn o.i. geen objectief in de natuur gegeven realiteiten, geen echte eenheden, zoals soorten, naar analogie waarvan ze opgesteld worden, dat wel zijn. De begrippen constant en trouw zijn zeer betrekkelijk. Ze doelen op zeer locaal bepaalde verschijnselen. Afgrenzing van de denkbeeldige eenheden, associaties, is door het voorkomen van vele geleidelijke overgangen niet objectief te verrichten. Vandaar dat we meer aandacht schonken bij een eerste orientatie aan dominantie van bepaalde soorten, soorten waarvan sommige een hoge indicatorwaarde (RAMENSKY) bezitten. Hieruit resulteert dus enigszins een tussenpositie tussen de Noordse en de Fr.-Zwitserse methode.

Vooral in verband met het optreden van *Calamagrostis neglecta* is een vergelijking van de *Carex diandra*-vegetaties met die in Oost-Pruisen en Polen te trekken. Het blijkt dan dat in genoemde gebieden dergelijke vegetaties een sterker continentale inslag hebben, trouwens *Cal. neglecta* kan ook als een subarctisch continentale soort beschouwd worden. In Lapland treedt hij in totaal andere vegetatietypen, rijk aan arctisch-alpiene soorten sterk op! Naast de geographische variatie kan men bij het *Carex diandra*-vegetatietype ook een oecologische variatie waarnemen.

De samenstelling van de lijst van begeleidende soorten blijkt nl. voor een deel van de oecologische gesteldheid van het betrokken gebied af te hangen.

In aansluiting op het voorgaande is een methode op te stellen voor vergelijkend sociologisch georienteerd onderzoek in moerasgebieden. Deze methode gaat uit van opname-materiaal verkregen met de Fr. Zwitserse opname-techniek. Dat materiaal wordt dan zo verwerkt dat de affiniteit (mate van samengaan, koppeling bij DE VRIES en SCHEYGROND) van bepaalde soorten t.o.v. elkaar in bepaalde gebieden vastgesteld wordt. Daarnaast worden overeenkomstige successiestadia uit verschillende gebieden met elkaar vergeleken. Uit dat alles zijn dan conclusies te trekken over de combinaties die in bepaalde milieuconstellaties voorkomen, over het gedrag van afzonderlijke soorten t.o.v. bepaalde milieufactoren als grondwaterstand, pH, bicarbonaatgehalte van het uitgangsmilieu e.d., en over eventueel optredende verschillen in affiniteiten, bepaald in verschillende gebieden. Een dergelijke meer exacte methode van onderzoek en verwerking van de resultaten kan ons probleemstellingen over de autoecologie verschaffen. Tevens moet dan natuurlijk ook op concurrentiekracht en verspreidingstype gelet worden.

Daarna kunnen we dan, uitgaand van exactere kennis van de oecologie van de afzonderlijke soorten, een betere verklaring vinden voor plantensociologische wetmatigheden, op analoge manier dus als D. M. DE VRIES dat bij het graslandonderzoek nastreeft. Dit alles onder het motto van IVERSEN (1936):

> „Das Zentrale Problem in der Vegetationsforschung ist die oekologisch bedingte Gesetzmässigkeit in der Zusammensetzung der Vegetation”.

Vervolgens sprak de heer H. TJ. WATERBOLK uit Groningen over:

De Betekenis van het Kruidenpollen voor het Palynologisch Onderzoek.

De mogelijkheid tot ruimere toepassing van de analyse van het kruidenpollen wordt door een aantal factoren bepaald.

1. In de verschillende sedimenten zal slechts pollen van de lokale vegetatie en van anemophiele kruiden uit de omgeving verwacht kunnen worden. Van beide groepen blijkt de aanwezige hoeveelheid zo gering te zijn, dat de normale boompollensom van 150 onvoldoende is en men tot 500, liefst 1000 moet gaan;
2. Van een minder goede conservering van het kruidenpollen schijnt in het algemeen geen sprake te zijn;
3. Voor een zekere determinatie is in vele gevallen het gebruik van een immersieobjectief noodzakelijk, terwijl tevens een scherp inzicht in de morphologie van de pollenexine is vereist. Men dient bijv. te onderscheiden of deze opgebouwd is uit één, dan wel twee lagen (resp. entexine en ectexine). De ectexine bestaat meestal uit columellae, die aan de top tot een tectum zijn vergroeid. Op dit tectum kunnen zich opnieuw allerlei uitsteeksels bevinden. Van belang is bijv. of een reticulate pollenkorrel tectaat of intectaat is (secundair, resp. primair reticulum). Ingewikkelde structuren en sculpturen komen voor. Zo heeft *Succisa* vertakte columellae en twee typen echinae (stekels) op het tectum. Bovendien zijn de columellae enigszins netvormig gerangschikt, IVERSEN en FAEGRI hebben een determinatietabel uitgewerkt, welke op deze en overeenkomstige kenmerken berust, doch alleen gebruikt kan worden samen met een collectie praeparaten van recent materiaal.

In de regel kan men de familie bepalen, waartoe een gevonden korrel behoort, vaak ook secties binnen de familie, minder vaak het geslacht en slechts zelden de soort. Zo onderscheidt men binnen de *Compositae* de groepen *Tubuliflorae* en *Liguliflorae*, doch daarnaast het geslacht *Artemisia* en de soort *Centaurea cyanus*; binnen de *Umbelliferae* alleen *Hydrocotyle*. Daarentegen kan men binnen het geslacht *Plantago* de soorten *maritima*, *coronopus*, *lanceolata* en *major* + *media* determineren.

Fraaie resultaten met behulp van het kruidenpollen zijn verkregen door de Deense onderzoekers, speciaal door IVERSEN. Zij betreffen in de eerste plaats een scherpere plantensociologische karakterisering van het milieu. Zo blijken in Deense fjordsedimenten de mariene perioden te onderscheiden door het veelvuldig optreden van *Ruppia*-pollen. Laatglaciale meersedimenten in ons land bevatten pollen van

Sparganium, *Typha*, *Potamogeton*, *Myriophyllum*, *Nymphaea* etc. In *Sphagnum*veen kan men *Utricularia* ontmoeten.

In de tweede plaats kan het gevonden kruidenpollen dienen ter nadere karakterisering van de vegetatie in de omgeving. Zo kon IVERSEN op grond van de curven van *Hedera*, *Viscum* en *Ilex* zijn inzicht in de klimatologische achtergrond van de postglaciale vegetatieveranderingen vergroten. *Hedera* en *Viscum* zijn beide sterk vertegenwoordigd in het Atlanticum.In het subboreaal gaat *Hedera* echter achteruit, wat IVERSEN wijt aan koudere winters. Bij het begin van het subatlanticum is ook *Viscum* vrijwel verdwenen, doordat nu ook de zomertemperatuur gedaald zou zijn. Daarentegen wijst de uitbreiding van *Ilex* op grotere vochtigheid.

JESSEN kon een bijdrage leveren tot de oplossing van typisch plantengeografische problemen. Hij vond in een Iers veen pollen van *Eriocaulon septangulare*, één van de weinige Amerikaanse elementen in de Ierse flora.

Bijzonder interessant zijn IVERSEN's onderzoekingen naar de invloed van de mens op het landschap in voorhistorische tijd. De nabijheid van een mesolithische nederzetting in het binnenland is niet zelden te merken aan het optreden van *Chenopodiaceae*-stuifmeel. De komst van *Plantago lanceolata* en een sterke uitbreiding van *Artemisia* blijken samen te gaan met de neolithische akkerbouw. In het afgelopen jaar is op verschillende plaatsen in Denemarken zelfs stuifmeel van *Vitis* gevonden, juist in niveaux van intensieve neolithische akkerbouw en veeteelt.

Daarna verkreeg de heer B. A. DE PLANQUE (Utrecht) het woord; zijn voordracht was getiteld:

Palynologisch Onderzoek van het Holoceen en Laat-Glaciaal (met Alleröd-schommeling) in Zuid-Oost Friesland.

Micro-analytisch onderzoek van hoogveenprofielen uit Z.O. Friesland bracht aan het licht dat *Fagus* al voor de grenshorizon voorkomt. Hetzelfde vonden Eshuis in Z.O. Groningen en FLORSCHÜTZ & WASSINK te Vriezenveen. Dit in tegenstelling met het meer algemeen voorkomende geval, dat *Fagus* in of kort na de grenshorizon begint op te treden.

Verder bleek dat bij de *Pinus-Alnus*kruising *Betula* dominant is over *Pinus*.

De opvallende toename van de *Ericaceae*-percentages in de oppervlakkige lagen tot hoge waarden (800—1660%) wordt uitgelegd als een gevolg van een toenemende begroeiing met hei van de wijdere omgeving (onder deze laatste niet het omliggende, mogelijk uitgestrekte veen begrepen).

Een Allerödschommeling werd vervolgens aangetoond bij de analyse van een laagveenprofiel. Een diagram, opgemaakt volgens de oude methode kon vergeleken worden met dat van het Bolleveen (Dr.) van WATERBOLK. De gelijkenis is groot. Een tweede diagram, geconstrueerd volgens IVERSEN, maakte vergelijking mogelijk met dat van het Hykermeer (Dr.) van V. D. HAMMEN. De Allerödschommeling met de Oudere *Dryas*laag eronder en de Jongere *Dryas*laag er boven kan op dezelfde gronden worden aangenomen. Evenwel ontbreekt een duidelijke meer organogene afzetting. Opmerkelijk is echter dat een afnemende bruinkleuring van het zand (als van ijzeroer) eindigt bij het begin van de Allerödschommeling. Een duidelijke Böllingoscillatie ontbreekt. Als nieuw werd gevonden, uitsluitend voorkomend in de Oudere *Dryas*lagen, het pollen van *Polygonum amphibium.*

De onderzochte venen werden ons aangewezen door de heer SIEBINGA, arts te Opeinde (Friesland).

De laatste spreker was de heer M. SANDERS uit Wageningen, die mede namens Dr D. M. DE VRIES sprak over:

De Soortenrijkdom van Graslanden in verband met de Standplaats.

De rijkdom aan soorten werd nagegaan uit de aanwezige soorten in de monsters voor het type-onderzoek der Nederlandse graslanden van DE VRIES, welke monsters zijn genomen volgens de $\frac{1}{4}$ dm^2-frequentie-methode. Het absolute aantal soorten per perceel kan dus niet opgegeven worden. Om een inzicht te krijgen omtrent de waarde der cijfers hebben we deze methode vergeleken met die van 100 m^2-opnamen. In 16 percelen, waar beide methoden werden toegepast, vonden we gemiddeld 35 en 37 soorten, respectievelijk met de $\frac{1}{4}$ dm^2-frequentie-methode, waarbij meestal 100 plukjes per perceel werden genomen, en met de 100 m^2 methode. Het verschil is dus opmerkelijk gering, vooral als we bedenken, dat bij de laatste methode een 400 maal zo groot oppervlakte wordt onderzocht. Uiteraard geldt deze vergelijking alleen voor homogene percelen. Ter orientering volgen hier eerst enkele algemene cijfers. Zo vonden we in de monsters maximaal 64 en minimaal 13 soorten. Gemiddeld over 632 monsters was het aantal soorten 31. Hierbij werden de kwelders buiten beschouwing gelaten. Door de zeer extreme levensvoorwaarden, welke hier heersen, daalt het aantal soorten nog aanmerkelijk en wel op lage kwelders tot 7 en 8 en op hoge tot 5. Beschouwen we nu het aantal soorten bij verschillende phosphaattoestanden, dan zien we een mooi verband en wel bij stijging van de P-toestand van slecht naar goed, daalt het aantal soorten van 38 tot 28. Bij de kali-toestand is de daling nog iets sterker en wel van 38 tot 26. Een goede bemestingstoestand mogen we dan ook wel als extreem beschouwen.

Bij stijging van de pH zien we ook het aantal soorten stijgen. Van zeer sterk zuur ($pH<4$) tot alcalisch liep het aantal soorten op van 20 tot 35. Weinig verschillen in soortenrijkdom bleken te bestaan bij de verschillende grondsoorten en vochtigheidsgraden. Wel trad weer een duidelijke daling op bij steeds intensievere beweiding. Bij echte hooilanden, die nimmer geweid worden, was het aantal soorten 37, bij zuivere weiden 28.

Door het toepassen van een zeer eenvoudige polyfactor-analyse bleek ons, dat de bemestingstoestand de voornaamste factor is en dat de gebruikswijze op de tweede plaats komt.

Ten slotte werd nagegaan, of er verband bestaat tussen het aantal soorten en de mate van dominantie. Proeven van Osvald in Zweden en ook van Ahlgren en Aamodt in Amerika toonden het afscheiden van remstoffen door de wortels der grassen aan. We vonden ook een daling van het aantal soorten, indien het gewichtsaandeel van de dominerende soort toeneemt, maar in hoeverre dit te wijten is aan de invloed der leidende soort of aan andere factoren, is vanwege het nog te geringe aantal waarnemingen niet met zekerheid te zeggen.

Daarna werd, met een woord van dank tot de sprekers en bezoekers, de vergadering door de voorzitter gesloten.

JAARVERSLAG van de Commissie voor de Phytopathologie over 1949.

In de commissie kwam wijziging door het aftreden van Mej Dr M. P. de Bruyn Ouboter, die niet herkiesbaar was en door het bedanken van Dr C. Wehlburg wegens vertrek naar het buitenland. In de vacatures werd voorzien door de benoeming resp. van Dr A. J. P. Oort en Mevr. G. de Bruin-Brink. De commissie bestaat thans uit de leden Dr A. J. P. Oort (voorzitter), Mevr. G. de Bruin-Brink (secretaresse), Mej. Dr C. H. Klinkenberg, Dr J. W. M. Roodenburg en Drs F. Tjallingii.

Op 22 October 1949 werd te Utrecht een middagvergadering gehouden, waar de Heer P. A. Florschütz sprak over gezwelvorming bij planten en Dr T. J. Barendregt over Dierlijke tumoren.

Het aantal contribuanten bedroeg per 31 Dec. negen. Drie nieuwe contribuanten gaven zich reeds op voor 1950.

Wageningen, Dec. 1949. Voor de secretaresse:
Dr A. J. P. OORT.

JAARVERSLAG van de Commissie voor de Plantenphysiologie 1949

De commissie voor de plantenphysiologie vergaderde in 1949 drie maal. De eerste vergadering vond plaats 5 Maart om 14.00 uur in het Botanisch Laboratorium te Leiden. Aanwezig waren 28 leden. De Heer J. A. HIJNER sprak over: „De invloed van vitaminen op een *Rhizoctonia* spec. van een *Cymbidium* spec. in verband met de Orchideeënsymbiose.". Tevens deelde de Heer HIJNER iets mede over zijn bezoek aan het „Californian Institute for Technology" te Pasadena.

De tweede vergadering werd gehouden 7 Mei om 14.00 uur in het Botanisch Laboratorium te Utrecht. Aanwezig waren 39 leden. De Heer J. RIETSEMA sprak over: „De invloed van de pH op de werking van groeistof" en de Heer P. FLORSCHÜTZ over: De werking van trijoodbenzoëzuur op de groei".

De derde vergadering werd gehouden 17 December om 14.00 uur in het Hugo de Vries Laboratorium te Amsterdam. Aanwezig waren 42 leden. Dr B. J. D. MEEUSE sprak over: „Enige onderzoekingen over fermentatie en ademhaling in erwtenkiemplanten" en mej. VAN ANDEL over: „De invloed van licht en suiker op de opname van kalium en phosphaat bij mais."

In de vacature ontstaan door het periodiek aftreden van prof. Dr A. W. H. van HERK werd voorzien door benoeming van ondergetekende.

Amsterdam, Dec. 1949. De Secretaris van de Commissie:
Dr A. QUISPEL.

VERSLAG van de Commissie voor de Plantensystematiek en Plantengeografie over het jaar 1949.

In de samenstelling van de Commissie ontstond een wijziging doordat Mejuffrouw Dr CH. H. ANDREAS vervangen werd door Dr F. P. JONKER, die in plaats van Mej. ANDREAS eveneens belast werd met het secretariaat.

De Commissie organiseerde in het verslagjaar één vergadering op Zaterdagmiddag 29 October, in de collegezaal van het Hugo de Vries-laboratorium te Amsterdam. Deze vergadering werd bijgewoond door 38 personen. De agenda vermeldde 6 wetenschappelijke mededelingen, n.l. door Mej. Dr J. TH. KOSTER: „Over de verspreiding van enige Nederlandse Wieren", P VAN ROYEN: „DE genera *Oenone* en *Apinagia* (*Podostemonaceae*)", Dr S. J. VAN OOSTSTROOM: „Over oude afbeeldingen van *Proteaceae*", P. A. FLORSCHÜTZ: „Enkele problemen bij de bestudering van de Surinaamse Mosflora", Dr C. G. G. J. VAN STEENIS: „*Nothofagus* op Nieuw Guinea" en Dr H. C. D. DE WIT: „JACOBUS BONTIUS". Na iedere voordracht volgde een levendige gedachtenwisseling en uit de vergadering kwam de wens naar voren dat de Commissie zou trachten in het komende jaar twee bijeenkomsten te organiseren. De voorzitter, Dr LAM, sprak namens de vergadering na de voordracht van Dr VAN STEENIS enkele woorden van afscheid tot deze spreker in verband met zijn aanstaand vertrek naar Buitenzorg.

Aan deze vergadering ging een korte commissievergadering vooraf.

Utrecht, Dec. 1949.

De Secretaris,
Dr F. P. JONKER.

DE CONTACT COMMISSIE VOOR NATUUR- EN LANDSCHAPSBESCHERMING EN DE VOORLOPIGE NATUURBESCHERMINGSRAAD

Voordracht gehouden door Dr. Th. Weevers in de Jaarvergadering 30 Jan. 1949

De uitnodiging van U, mijnheer de Voorzitter, hier hedenmorgen te spreken over de Contact Commissie voor Natuur- en Landschapsbescherming werd door mij met genoegen aanvaard. Echter was ik van mening, dat het nodig was ook de Natuurbeschermingsraad in deze bespreking te betrekken.

Ik zeide „met genoegen aanvaard” omdat dit mij de gelegenheid biedt, als het ware rekenschap af te leggen van mijn taak als een vertegenwoordiger der Botanische Vereniging in deze Contact Commissie. Ik heb deze funktie nu ruim 12 jaar naar mijn beste weten vervuld en het is dus tijd, dat ik daarover verantwoording afleg.

Het was in het jaar 1932, dat de bedreiging van het Geuldal bij Epen, waar plannen bestonden om een deel van het dal tot een waterbassin te maken, de aanleiding werd tot de instelling der Contact Commissie. Het waren de Vereniging tot Behoud van Natuurmonumenten, de Natuurhistorische Vereniging, de Entomologische Vereniging, de Hydrobiologische Club, de Vereniging tot Bescherming van Vogels, het Limburgs Landschap, de A.N.W.B. en Heemschut, die gehoor gaven aan de oproep der Botanische Vereniging om een aktie voor het behoud van het Geuldal te gaan voeren. Het zal U wel bekend zijn, dat door verschillende oorzaken het Geuldal gespaard bleef; de Commissie werd echter niet ontbonden, maar bleef bestaan en was werkzaam op het gebied der natuurbescherming over het gehele land. Geleidelijk nam het aantal Verenigingen, die lid van de Commissie werden, toe en in 1946 was dit aantal tot ruim 70 gestegen, waarvan echter nog steeds de A.N.W.B. en de Vereniging tot Behoud van Natuurmonumenten de grootste en tevens de meest kapitaalkrachtige zijn.

De Contact Commissie is dus geen officieel lichaam, geen organisatie van staatswege, zoals met de Natuurbeschermingsraad wèl het geval is, maar hierover later meer.

Het werk der Contact Commissie moet zich dus bepalen tot de verbreiding der natuurbeschermingsgedachte, tot het geven van adviezen aan en het richten van adressen tot officiële en partikuliere lichamen en personen. Zij heeft daartoe verschillende werkgroepen ingesteld en geeft een geïllustreerd tijdschrift uit getiteld „Natuur en Landschap”.

De naam „Contact Commissie voor Natuurbescherming” werd enige jaren geleden gewijzigd in die van „Contact Commissie voor Natuur- en Landschapsbescherming”. Daardoor wordt tot uitdrukking gebracht, dat ook de zorg voor het Landschap, voor de Nederlandse Cultuurlandschappen tot haar taak behoort.

Oorspronkelijk werden door een aantal der grotere Verenigingen vertegenwoordigers benoemd om in het bestuur der Contact Commissie zitting te nemen, maar langzamerhand is het met dit bestuur zo gegaan als in de Regententijd met allerlei kolleges het geval was, n.l. dat zij zichzelf aanvulden met personen, die om de een of andere reden geschikt werden geacht. Zo zitten ook in het bestuur der Contact Commissie nu een aantal personen, die hun krachten willen wijden aan de natuur en landschapsbescherming in ons land, zonder dat zij als vertegenwoordigers van bepaalde verenigingen te beschouwen zijn. In de tegenwoordige tijd is Mr M. VAN DER GOES VAN NATERS voorzitter, Mr Dr P. G. VAN TIENHOVEN onder-voorzitter, Ir W. G. VAN DER KLOOT en Mr H. P. GORTER secretarissen, Dr W. C. DE LEEUW penningmeester.

Leden van het bestuur zijn verder de Heren G. A. BROUWER, H. C. CLEYNDERT A.zn, J. DRIJVER, Mr J. LINTHORST HOMAN, F. K. OZINGA, Dr C. VAN RIJSINGE, Mr C. J. VAN SCHAARDENBURG, Mr. STAN SMEETS, Dr V. WESTHOFF en spreker.

Laat ik alvorens verder te gaan U duidelijk trachten te maken, hoe mijn houding in het Bestuur is geweest, welk standpunt ik daar ingenomen heb. Om het in enkele woorden te zeggen: mijn houding is die geweest, welke naar mijn mening, de juiste was voor een vertegenwoordiger der Botanische Vereniging, d.w.z. dat ik mij voelde als de voorvechter van de belangen der wetenschap bij de natuurbescherming.

Het zal wel niet nodig zijn hier uiteen te zetten, dat voor de studie der botanie in de ruimste zin van het woord, het onmisbaar is, dat er in ons land terreinen worden aangetroffen, die als natuurlijke terreinen kunnen beschouwd worden. Natuurlijk ten minste in zover, dat het ingrijpen van de mens geen diepgaande wijziging in de daar van nature voorkomende plantenassociaties heeft gebracht. Of zo dit laatste wèl het geval is, hierdoor niet anders gebeurd is, dan dat een normaliter tijdelijk en voorbijgaand stadium der successie zoals b.v. de heide tot een blijvende toestand is geworden.

Misschien vereist het zo juist genoemde enige toelichting. Zoals reeds werd gezegd is de naam der Commissie veranderd in die voor Natuur- en Landschapsbescherming. Deze toevoeging wijst op een zich ook speciaal bezig houden met de cultuurlandschappen. Dat kan zeer goed gepaard gaan met het ijveren voor het behoud van terreinen, die uit een natuurwetenschappelijk oogpunt van belang zijn, maar het kan ook, dat de belangen van de laatste soort, waarbij de terreinen zoveel kleiner van omvang zijn, daardoor in het gedrang komen.

Nu wil ik volstrekt niet zeggen, dat in concrete gevallen mijn houding in al die jaren precies dezelfde gebleven is. In de eerste plaats is de strijd voor het behoud van de botanisch belangrijke terreinen een kwestie van taktiek, van het kiezen van de beste weg uit de verschillende mogelijkheden, dikwijls helaas ook van de weg, die het minst slecht is. Maar bovendien: mijn inzicht in de maatregelen nodig voor de natuurbescherming in ons land heeft zich in enkele opzichten gewijzigd. Toen ik nu ruim 20 jaar geleden benoemd werd in de „Commissie van Advies inzake de Natuurmonumenten van het Staatsbosbeheer" moest ik om zo te zeggen de praktijk van het beschermen der natuur in ons land nog leren. Ook de ontwikkeling van de plantensociologie heeft mijn inzichten gewijzigd en verruimd. Om één voorbeeld te noemen: terwijl vroeger op de vraag hoe een terrein als het Korenburgerveen als natuurmonument behandeld moest worden, het antwoord eenvoudig luidde: „Laat het terrein aan zijn lot over en laat de natuur ongestoord haar gang gaan", zou nu het advies zeker niet meer zo uitvallen. Het zou ons echter te ver voeren hier dieper op in te gaan.

Het zal wel duidelijk zijn, dat het ondoenlijk zou wezen om hier alles te memoreren, wat in de afgelopen jaren door de commissie is gedaan. Ik zal mij dan ook bepalen tot de laatste jaren; wat betreft de tijd vóór 1943 kan ik bovendien verwijzen naar een stukje van mijn hand in het „Vakblad voor Biologen" van Juni 1943.

Menigmaal werd ondanks veel moeite het doel niet bereikt en moest men zich tevreden stellen met het woord van Propertius „in magnis et voluisse sat est", of vrij vertaald „Men rekent de uitslag niet, maar telt het doel alleen." Zo ligt in dit verband het woord „St. Pietersberg" ons op de lippen, maar ook de aktie voor het behoud van het Beerzedal in Brabant is niet met sukses bekroond, terwijl in verschillende gevallen zoals in Noordwest-Overijsel, in Noordoost-Twente de kwesties nog op een oplossing wachten, evenzeer als dit met de zo merkwaardige blauwgraslanden het geval is.

Naast andere punten van belang zoals het behoud van de ongerepte delen van de Veluwe, waartoe een Veluwedag in Apeldoorn gehouden werd, gevolgd door een adres aan de Ministerraad, is het vooral de verhouding van de natuur- en landschapsbescherming ten opzichte van de landbouw, die in de laatste tijd de aandacht van de Contact Commissie bezig houdt.

In een land als het onze, waar nagenoeg geen woeste gronden meer zijn, tenminste geen woeste grond, die voor bebouwing of andere ontginning in aanmerking komt, waar de bevolkingsdichtheid groter is dan elders in West-Europa en nog steeds toeneemt, daar moet die strijd voor het behoud van de laatste resten der oorspronkelijke wilde natuur wel uitermate zwaar zijn. Moeilijk is die strijd ook omdat bij hen, die met de techniek der ontginningen belast zijn, zo dikwijls alle begrip voor de biologische waarden ontbreekt.

De zich voordurend uitbreidende steden, de onvermijdelijke wegenaanleg, nemen goede bouwgronden in beslag, de stedelijke bevolking eist terreinen voor recreatie, terwijl de boer vecht voor meer bouwgrond. Zo raakt de wilde flora in het gedrang, steeds meer verdwijnen de voor ons zo kostbare woeste gronden, de verplichting tot aanmelding indien het de ontginning van gronden betreft, die op de lijst van het Nationale Plan zijn geplaatst, geeft lang niet altijd baat. Een goede natuurbeschermingswet is een dringende eis, maar daarover straks.

Men kan nu bij die botsing van belangen tussen natuurwetenschap en recreatie enerzijds, landbouw met ruilverkaveling anderzijds, twee wegen inslaan. De keus gaat tussen strijd tot het uiterste en een compromis. Doelbewust heeft de Contact Commissie de laatste weg gekozen en getracht dit alles van uit een ruimer, als het ware hoger gezichtspunt te bezien, n.l. dat van het nationaal belang, het belang van het volk als geheel. Dit belang eist enerzijds een zo groot mogelijke produktie in deze tijd waarin het woord deviezen ons in de mond bestorven ligt weten wij dit allen maar al te goed. Maar anderzijds is het een nationaal belang dat de stedelijke bevolking de natuurruimte krijgt, die zij voor haar ontspanning behoeft, dat de natuurwetenschap de beschikking houdt over de terreinen, die voor haar onmisbaar zijn. Het is onnodig, dit op deze plaats breder uiteen te zetten.

Nadat door een paar leden van de Commissie een rapport was opgemaakt over landbouw en natuurbescherming, waarin een aantal stellingen geponeerd waren, werd dit in de Commissie uitvoerig besproken met het resultaat, dat ten slotte overeenstemming bereikt werd over de vraag hoe die coördinatie van landbouw en natuurbescherming het best te bereiken zou zijn. Daarop volgde een bespreking in het Huis te Eerbeek in de afgelopen zomer, waar zowel van de kant der Contact Commissie als door vooraanstaande personen uit de Nederlandse Landbouwgemeenschap de kwestie werd belicht. Het resultaat hiervan was, dat er nu een contact tussen beide organisaties tot stand is gekomen en de kans op het bereiken van een compromis is vergroot.

Het zou ons te ver voeren al die stellingen hier te behandelen, alleen wil ik naar voren brengen, dat van de zijde van de wetenschap vooral de nadruk is gelegd op het behoud van die terreinen die onvervangbaar zijn. Dat zijn de in eerste plaats de natuurlijke landsschapstypen, die voor bepaalde delen van ons land kenmerkend, soms uniek zijn, ja zelfs uniek kunnen zijn voor geheel West Europa. Ongetwijfeld neemt de natuurbeschermer hierbij een zeer bescheiden standpunt in maar is het m.i. toch juist, dat wat het belangrijkste is, het meest naar voren is gebracht.

Maar het wordt tijd over te gaan tot het 2e deel van ons onderwerp: „de voorlopige Natuurbeschermingsraad”. De toevoeging „voorlopige” is slechts het gevolg hiervan, dat zodoende de instelling van de raad alleen een koninklijk besluit vereiste. De Raad werd na de oorlog in 1945 ingesteld door de Minister van Onderwijs, nadat „de Centrale Commissie voor Natuurbescherming,” waarin Mr Dr BEUMER, Mr VAN TIENHOVEN en Dr VAN STEYN zitting hadden, was opgeheven.

Tot voorzitter van de Raad werd benoemd Mr Dr W. G. A. VAN SONSBEEK, tot lid en ondervoorzitter Prof. Dr G. J. VAN OORDT tot lid en secretaris Mr M. VAN DER GOES VAN NATERS.

Leden zijn de Heren Jhr W. H. DE BEAUFORT, H. C. CLEYNDERT AZN., H. MANDERS, Mr Dr VAN TIENHOVEN en schrijver dezes. Ambtshalve lid zijn de Directeur van het Staatsbosbeheer (Dr J. A. VAN STEYN), de Directeur van de Rijksdienst voor het Nationale Plan (Dr Ir F. BAKKER SCHUT), terwijl Mr J. K. VAN DER HAAGEN, hoofd van de Afdeling Oudheidkunde en Natuurbescherming van het Ministerie van Onderwijs, Kunsten en Wetenschappen het recht heeft alle vergaderingen bij te wonen.

De taak van de Raad is in het kort gezegd een tweeledige: in de 1e plaats is de Raad belast met de voorbereiding van de zo dringend nodige „Natuurbeschermingswet”. In de 2e plaats is haar taak het geven van adviezen aan de Minister van Onderwijs, waarbij op de voorgrond gesteld moet worden, dat de Raad de bevoegdheid bezit om ook ongevraagd adviezen in te dienen. Belangrijk is dit vooral, waar het betreft de aankoop van natuurwetenschappelijk unieke terreinen met gelden door het Rijk hiervoor beschikbaar gesteld.

Tegelijk met de Raad werden verschillende Commissies ingesteld, waarin naast enkele leden van de Raad ook niet-leden, deskundig op het betreffende gebied, zitting hebben. Zo is er een juridische commissie onder het voorzitterschap van Prof. Mr Dr C. W. van der Pot, die speciaal belast is met de voorbereiding van de Natuurbeschermingswet. Naar verluidt, ikzelf heb geen zitting in deze commissie, is zij reeds in belanrijke mate met haar taak gevorderd. Dan is er een „vogelbeschermingscommissie" onder voorzitterschap van Prof. van Oordt en een „natuurwetenschappelijke commissie", waarvan spreker de voorzitter is.

Deze laatste is in zekere zin de voortzetting van de erin geincorporeerde „Commissie van advies inzake de Natuurmonumenten van het Staatsbosbeheer".

Zij geeft eventueel na onderzoek ter plaatse adviezen zowel aan de Raad als aan de Directeur van het Staatsbosbeheer, adviezen, die allerlei vragen betreffende de natuurwetenschappelijk belangrijke terreinen raken. Wanneer wij eens even een kijkje nemen in een dergelijke commissievergadering, dan komen daar b.v. de volgende punten aan de orde:

1. de vraag, hoe het beste paal en perk te stellen is aan een ongewenst, te druk bezoek aan een of ander natuurmonument van het Staatsbosbeheer.
2. de vraag of het wenselijk is een bepaald natuurmonument uit te breiden.
3. de vraag of weer een ander terrein van het Staatsbosbeheer van zodanige betekenis is, dat erop aangedrongen moet worden het tot natuurmonument te verklaren.
4. de kwestie of in de een of andere ruilverkaveling belangrijke terreinen met interessante plantenassociaties voorkomen, die zo mogelijk ongerept moeten blijven.

U ziet, dat hier voor de natuurbescherming zeer belangrijke vragen aan de orde gesteld worden.

Ten slotte is er nog een kleine „inventarisatie commissie", bestaande uit Ir. G. A. Overdykink, Ir W. G. van der Kloot en mijzelf. Deze houdt zich nu al jaren bezig met de inventarisatie der terreinen in ons land, die uit het oogpunt van natuur en landschap van belang zijn. Zo ogenschijnlijk lijkt dit een eenvoudige taak, temeer omdat door het Staatsbosbeheer reeds een inventarisatie van het natuurschoon in verschillende delen van ons land heeft plaats gehad. Maar deze inventarisatie was slechts ten dele op sociologische leest geschoeid, was niet volledig en voor sommige delen van ons land verouderd. Het zal later duidelijk worden, dat voor het doel waarvoor zij dienen moeten de opgaven van de merkwaardige terreinen topographisch volkomen verantwoord moeten zijn. Reeds in 1942 was een voorlopige lijst opgemaakt en ingediend bij het bureau van de Rijksdienst van het Nationale Plan. De President van het Nationale Plan heeft die lijst in de Staatscourant geplaatst met de bijvoeging, dat in deze terreinen geen werken mogen uitgevoerd worden zonder dat hiervan kennis is gegeven aan de Directeur van de Rijksdienst van het Nationale Plan. De President van het Nationale Plan kan zijn veto erover uitspreken nadat vóór en tegen overwogen is. Plaatsing op de bedoelde lijst vrijwaart dus voor verrassingen op dit gebied, maar geeft geen absolute vrijwaring van aantasting van het terrein.

Deze voorlopige lijst was zeer onvolledig en de Commissie is nu al geruime tijd bezig met het bewerken van een definitieve lijst, waarin de grenzen van elk terrein zo grondig mogelijk op de stafkaart worden vastgelegd, terwijl tevens door een korte aanduiding wordt gezegd in welk opzicht het terrein merkwaardig is. Daarbij wordt een onderscheid gemaakt tussen de wetenschappelijke en de landschappelijke of de recreatieve waarde. Aan die met landschappelijke of recreatieve waarde wordt toegevoegd of de betekenis nationaal of regionaal is. Die van lokaal belang worden niet op de lijst geplaatst; hun behoud moet door streekplannen geregeld worden. Terreinen die van wetenschappelijke betekenis zijn, worden steeds beschouwd als te zijn van nationaal belang.

De lijsten worden provinciegewijs gemaakt en zijn gerangschikt volgens de stafkaart. Nadat de commissie klaar is, worden de lijsten eerst ter visie gelegd, zodat het voor verschillende instanties mogelijk is om opmerkingen of aanvullingen te geven. Dan gaan zij weer naar de commissie van drie terug, die overweegt of er nog wijzigingen nodig zijn. Tenslotte, na de Raad gepasseerd te zijn, komen de lijsten dan in handen van de Directeur van het Nationale Plan en worden door de President in de Staatscourant geplaatst.

Het is duidelijk, dat ook hier de Natuurbeschermingswet regelend zal moeten ingrijpen, zodat het behoud van de terreinen, die voor het gehele volk van onschatbare waarde zijn nog beter gewaarborgd is. Laten wij hopen dat deze wet nu niet lang meer zal uitblijven. „Est periculum in mora,” zoals ik reeds in mijn jaarrede van 1938 heb betoogd.

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LEDENLIJST

Lijst van de Leden der
Koninklijke Nederlandsche Botanische Vereeniging

December 1950

BESTUUR.

Prof. Dr W. H. Arisz, *Voorzitter*	(aftr. 1951).
Prof. Dr J. Lanjouw, *Ondervoorzitter*	(aftr. 1952).
Prof. Dr A. W. H. van Herk, 1*ste Secretaris*	(aftr. 1955).
Mej. Dr A. Jaarsveld, 2*e Secretaresse*	(aftr. 1953).
Dr Ir A. W. Kloos Jr, *Penningmeester* 1)	(aftr. 1954).

COMMISSIE VAN REDACTIE VOOR HET RECUEIL DES TRAVAUX BOTANIQUES NEERLANDAIS

De Voorzitter der K.N.B.V., *Voorzitter*	(aftr. 1951).
Prof. Dr A. A. Pulle, *Secretaris*	(1922; aftr. 1955).
Prof. Dr W. H. Arisz	(1942).
Prof. Dr A. W. H. van Herk	(1947).
Prof. Dr T. H. van den Honert	(1947).
Prof. Dr V. J. Koningsberger	(1934).
Prof. Dr J. Lanjouw	(1950).
Prof. Dr P. A. Roelofsen	(1950).
Prof. Dr E. C. Wassink	(1948; aftr. 1952).
De Penningmeester der Kon. Ned. Bot. Ver.	(aftr. 1954).

COMMISSIE VAN REDACTIE VOOR HET NEDERLANDSCH KRUIDKUNDIG ARCHIEF

De 1ste Secr. der Kon. Ned. Bot. Ver., *Voorzitter*	(aftr. 1955).
W. van Dijk, *Secretaris*	(aftr. 1954).
Dr J. Th. Henrard	(1931; aftr. 1955).
Dr G. Kruseman	(1944; aftr. 1951).
De Penningmeester der Kon. Ned. Bot. Ver.	(aftr. 1954).

COMMISSIE VOOR DE BIBLIOTHEEK HET HERBARIUM EN HET ARCHIEF

Prof. Dr Th. Weevers, *Voorzitter*	(1944; aftr. 1953).
Prof. Ir J. L. van Soest, *Secretaris*	(1946; aftr. 1954).
Dr Ir A. W. Kloos Jr	(1925; aftr. 1952).
Dr S. J. v. Ooststroom	(1947; aftr. 1951).

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1) Gironummer der Kon. Ned. Bot. Ver. 93030, Dordrecht.

COMMISSIE VOOR HET FLORISTISCH ONDERZOEK VAN NEDERLAND

Dr Ir A. W. Kloos Jr, *Voorzitter*	(1916; aftr. 1953).
Dr P. Jansen, *Secretaris*	(1914; aftr. 1954).
Jan G. Sloff	(1925; aftr. 1952).
Prof. Ir J. L. van Soest	(1935; aftr. 1951).
Th. J. Reichgelt	(1950; aftr. 1955).

SUBCOMMISSIE VOOR HET ZUIDERZEE-ONDERZOEK

Dr P. Jansen, *Voorzitter*	(1927; aftr. 1968).
H. W. E. Croockewit, *Secretaris*	(1946; aftr. 1963).
Ir J. Vlieger, *Archivaris*	(1937; aftr. 1954).
Dr Ir A. W. Kloos Jr	(1927; aftr. 1959).
Prof. Ir J. L. van Soest	(1927; aftr. 1960).
Jan G. Sloff	(1927; aftr. 1958).
Prof. Dr Th. J. Stomps	(1927; aftr. 1966).
Ir A. N. Koopmans	(1928; aftr. 1957).
Dr Ir. W Feekes	(1934; aftr. 1965).
Dr G. Kruseman	(1934; aftr. 1962).
Dr M. J. Adriani	(1937; aftr. 1970).
Mej. Dr K. J. Hocke Hoogenboom	(1937; aftr. 1952).
Dr A. Scheygrond	(1937; aftr. 1953).
Dr D. M. de Vries	(1937; aftr. 1970).
A. van der Werff	(1937; aftr. 1955).
A. C. Boer	(1943; aftr. 1961).
J. Meltzer	(1946; aftr. 1964).
D. Piet	(1947; aftr. 1967).
D. Bakker	(1948; aftr. 1969).
Mevr. Dr N. L. Wibaut—Isebree Moens	(1927).

COMMISSIE VOOR DE BESCHERMING VAN DE WILDE FLORA

Prof. Dr Th. Weevers, *Voorzitter*	(1927; aftr. 1952).
Jan G. Sloff, *Secretaris*	(1927; aftr. 1956).
Dr Ir A. W. Kloos Jr	(1927; aftr. 1951).
Ir J. Vlieger	(1944; aftr. 1953).
Dr Ir W. H. Diemont	(1947; aftr. 1955).
Dr V. Westhoff	(1946; aftr. 1954).
Prof. Dr J. Heimans	(1950; aftr. 1958).
H. Tj. Waterbolk	(1950; aftr. 1957).

COMMISSIE VOOR DE PHYTOPATHOLOGIE

Prof. Dr A. J. P. Oort, *Voorzitter*	(aftr. 1954).
Mevr. G. de Bruin-Brink, *Secretaresse*	(aftr. 1953).
Mej. Dr C. H. Klinkenberg	(aftr. 1951).
Dr J. W. M. Roodenburg	(aftr. 1952).
A. Slootweg	(aftr. 1955).

COMMISSIE VOOR DE BIOSOCIOLOGIE EN HET VEENONDERZOEK VAN NEDERLAND

Prof. Dr J. Heimans, *Voorzitter*	(aftr. 1952).
Dr F. P. Jonker, *Secretaris*	(aftr. 1951).
P. R. den Dulk	(aftr. 1951).
T. van der Hammen	(aftr. 1953).
Prof. Dr J. Lanjouw	(aftr. 1953).
H. T. Waterbolk	(aftr. 1951).
Dr. V. Westhoff	(aftr. 1953).

COMMISSIE VOOR DE PLANTENPHYSIOLOGIE

Prof. Dr V. J. Koningsberger, *Voorzitter*	(aftr. 1951).
Dr A. Quispel, *Secretaris*	(aftr. 1956).
Mej. Dr C. J. Gorter	(aftr. 1955).
Mej. Dr A. M. Hartsema	(aftr. 1952).
Prof. Dr T. H. van den Honert	(aftr. 1954).
Dr F. van der Paauw	(aftr. 1957).
Dr J. W. M. Roodenburg	(aftr. 1953).

COMMISSIE VOOR DE PLANTENSYSTEMATIEK EN PLANTENGEOGRAFIE

Prof. Dr H. J. Lam, *Voorzitter*	(aftr. 1951).
Dr F. P. Jonker, *Secretaris*	(aftr. 1955).
Prof. Dr J. Heimans	(aftr. 1954).
Prof. Dr J. Lanjouw	(aftr. 1952).
Dr S. J. v. Ooststroom	(aftr. 1953).
Prof. Dr H. J. Venema	(aftr. 1956).

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Dr A. F. Blakeslee (1924), Dept. of Botany, Smith College, Northampton, Massachusetts, U.S.A.

Prof. Dr O. Appel (1935), Irmgardstrasse 33, Berlin-Zehlendorff.

Prof. Dr J. Braun-Blanquet (1935), Station de Géobotanique, Chemin du Pioch de Boutonnet, Montpellier, Frankrijk.
Prof. Dr L. Buscalioni (1935), Istituto Botanico delle Universita, Bologna, Italië.
Prof. Dr A. Ernst (1935), Rigistrasse 54, Zürich.
Prof. Dr R. E. Fries (1935), Bergianska Trädgarden, Stockholm 50.
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Prof. Dr E. D. Merrill (1935), Gray Herbarium, Cambridge (Mass.), U.S.A.
Prof. Dr F. W. Oliver (1935), Department of Botany, Egyptian University, 8 Rue Sesostris, Heliopolis near Cairo, Egypte.
Prof. Dr D. N. Prjanischnikow (1935), Iwanowskaja 23, Moskou, U.S.S.R.
Prof. Dr Reddick (1935), Department of Botany, Cornell University Agricultural College, Ithaca (N.Y.), U.S.A.
Prof. Dr A. Frey—Wyssling (1948), Meilen bei Zürich.
Prof. Dr E. Gäumann (1949), Parkring 39, Zürich.

ERELEDEN

Dr P. Jansen (1902; 1945), Amsterdam Z., Fr. van Mierisstraat 128.
Dr Ir A. W. Kloos Jr (1912; 1945), Dordrecht, Nieuwe Weg 40.
Dr A. A. Pulle (1904; 1945), Baarn, Javalaan 5.
Dr Th. Weevers (1904; 1940), Amersfoort, Bergstraat 9.

GEWONE LEDEN [1]).

A. G. L. Adelbert (1938), Buitenzorg, Herbarium.
Dr M. J. Adriani (1931), Alkmaar, Papiermolenstraat 7.
E. Agsteribbe (1947), Amsterdam O., Galileiplantsoen 5 *hs.*
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Dr L. Algera (1927), Lisse, Schoolstraat 1.
Mej. Dr G. J. H. Amshoff (1935), Utrecht, Bot. Lab, L. Nieuwstraat 106.
Mej. O. M. van Andel (1946), Groningen, N. Kijk in 't Jatstr. 50*a*.
Mej. Dr Ch. H. Andreas (1932), Haren (Gr.), Rijksstraatw. 330.
Mevr. S. H. Anthoni-van Helsdingen (1934), Soekaboemi (Indonesia, Java) Selabatoeweg 32.

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[1]) Van adresveranderingen kennis geven aan de 1ste secretaris.

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Dr S. R. van Asperen de Boer (1921), Amsterdam Z., Jan van Eyckstraat 31.
Dr L. G. M. Baas Becking (1918), Nouméa, Nouvelle Calédonie.
Dr C. A. Backer (1944), Heemstede, Rembrandtlaan 13.
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D. Bakker (1941), Ens (N.O. Polder), Baan 6.
Dr Ir O. Banga (1947), Inst. v. Vered. v. Tuinb. gew., Wageningen, Herenst 25.
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Dr J. P. Bannier (1918), Wassenaar, Papegaaienlaan 15.
J. J. Barkman (1943), Leiden, Kamerlingh Onneslaan 21.
Ir J. E. Bausch (1940), Zwolle, Veerallée 33.
G. J. F. Becker (1947), Wageningen, Nude 18 .
Dr W. L. Beekman (1919) Enschede, Haverstraat 35.
Dr J. J. Beijer (1921), Lisse, Zwanendreef 10.
Dr W. Beijerinck (1925), Biol. Station, Wijster (Dr.).
P. J. Bels (1932), Houthem-St. Gerlach, Provinciale Weg 276.
Mevr. Dr H. C. Bels-Koning (1926), Houthem-St. Gerlach, Provinciale Weg 276.
Th. Belterman (1947), Haarlem, Jordenstraat 25.
J. Bennema (1946), Loenen a.d. Vecht. Rijksstraatweg 198A.
J. Bergmans (1937), Oisterwijk (N.Br.), B 25.
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Dr J. G. B. Beumée (1918), Bennekom, Edese Weg 123.
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Dr Ir J. T. P. Bijhouwer (1932), Bennekom, Dennelaan 3.
Dr S. Gj. Bloembergen (1930), Buitenzorg, Herbarium 's Lands Plantentuin, Java.
Mej. F. F. S. N. Bloemsma (1950), Utrecht, F. C. Dondersstraat 27.
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Dr B. K. Boom (1950), Nijmegen, van Oldenbarneveldstraat 32.
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Mej. M. Boshuizen (1933), Oegstgeest, Juffermansstraat 21.
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Dr H. P. Bottelier (1930), Naarden, Rijksweg 31.
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Dr J. Brand (1916), Doesburg, Phili Gastelaarstraat 21.
Dr P. J. van Breemen (1921), ’s-Gravenhage, de Bruynestraat 52.
Dr C. E. B. Bremekamp (1909), Utrecht, Botanisch Laboratorium, Lange Nieuwstraat 106.
Dr G. Bremer (1915), Wageningen, Geertjesweg 62.
Mevr. Dr D. E. Bremer-Reinders, (1932), Wageningen, Geertjesw. 62
Dr R. Brink (1946), Soerabaja, Komedieplein 1.
Mej. J. M. van Brink (1942), Utrecht, Prins Hendriklaan 106 (vac. Rotterdam C., Henegouwerlaan 16*a*).
Mej. E. Brinkman (1950), Leiden, Koninginnelaan 69.
Mej. H. Brinkman (1949), Groningen, Kraneweg 25*a*.
Fop. I. Brouwer (1948), Haren (Gron.).
G. A. Brouwer (1922), Bilthoven, de Genestetlaan 32.
H. F. J. v. d. Brugge (1949), Utrecht, Brigittestraat 22.
Mevr. G. de Bruin-Brink (1943), Utrecht, Maliebaan 127.
W. E. G. de Bruin (1945), Oosterbeek, Prins Hendrikstraat 1.
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Mej. J.G. Brunner (1943), Utrecht, J. v. Scorelstraat 17.
Mej. H. L. G. de Bruyn (1920), Wageningen, Hinkeloordseweg 5.
Mej Dr M. P. de Bruyn Ouboter (1937), Lisse, Herenweg 347.
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Mej A. H. v. d. Burg (1949), Groningen, Eendrachtskade 5.
A. C. J. Burgers (1946), Utrecht, Cathrijnesingel 28*bis*.
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Dr Joh. H. van Burkom (1903), Apeldoorn, Jachtlaan 134.
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Mevr. H. E. Casparé (1928), Rijswijk (Z.H.), Huis te Lande, van Vredenburchweg 150.
Dr J. ten Cate (1944), Amsterdam Z., Merwedeplein 15.

Dr B. J. Cholnoky (1948), Enkhuizen, Snouck van Loosen Park 17.
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Mej. Dr I. J. le Cosquino de Bussy (1928), Amsterdam Z., Quinten Massysstraat 18 *hs*.
Dr P. J. S. Cramer (1935), Wassenaar, Koninginneweg 10.
H. W. E. Croockewit (1940), Amsterdam Z., J. J. Viottastraat 27*hs*.
J. van Dalsum (1945), Leiden, Witte Rozenstraat 26.
Dr Ir H. G. Derx (1943), Directeur Treub-Laboratorium, Buitenzorg, Java.
Dr Ir W. H. Diemont (1936), Maastricht, Graaf van Waldeckstr. 41.
J. van Dijk Jr (1947), Amsterdam W., v. Hallstraat 133.
P. J. S. van Dijk (1937), Boskoop, Reijerskoop 221.
W. van Dijk (1932), Overveen, Julianalaan 66.
Dr S. J. Dijkstra (1932), Heerlen, Kloosterkoolhof 18.
Dr W. M. Docters van Leeuwen (1900), Leersum, Burgem. v. d. Boschlaan 159*a*.
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Dr M. A. Donk (1928), Buitenzorg, v. Limburg Stirumweg 17.
Ir J. Doorenbos (1948), Wageningen, Diedenweg 171.
Mevr. D. Dorsman-Stapel (1947), Amsterdam(C), Plantage Kerklaan 49*a*.
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Dr E. F. Drion (1930), 's-Gravenhage, Groenhovenstr. 14.
Dr Ir J. P. Dudok van Heel (1924), Naarden, „de Rietkraag".
Ir P. R. den Dulk (1944), Den Haag, Valkenboskade 206.
P. Dullemeyer (1948), Leiden, Falckstraat 2.
Mevr. H. Dutil—Voûte (1939), Makassar, p. a. Jacobson v. d. Berg & Co.
J. Mart. Duyven (1950), Oude Pekela.
C. O. Dwars (1948), Amsterdam, Rubensstraat 82.
W. A. van Eck (1950), Wageningen, Grindweg 197.
Dr Th. van Eek (1933), Amsterdam, p.a. Muysken, Apollolaan 193.
H. J. van Eekeren (1917), Zeist, Eikenlaan 2.
B. van Egmond (1935), Deventer, St. Jurrienstraat 8.
Mej. M. F. C. v. Egmond (1949), Utrecht, Maliebaan 100.
J. Engelen (1947), Groningen, Carolieweg 17*a*.
H. H. Evenhuis (1942), Wilhelminadorp, Lab. v. Zeelandsproeftuin.
M. L. Eversdijk (1919), Amsterdam Z., Minervalaan 12 *boven* (vac Biezelinge).
G. L. van Eyndhoven (1943), Haarlem, Floraplein 9.

Dr F. H. Feekes (1949), Baarn, Mollerusstraat 12.
Dr Ir W. Feekes (1931), Groningen, de Ranitzplein 3*b*.
F. C. J. Fischer (1950), Rotterdam, Lumeystraat 7*c*.
Mr Dr F. Florschütz (1920), Velp (G.), Enkweg 37.
P. A. Florschütz (1945), Utrecht, Anth. Matthaeusl. 30 *bis*.
Mevr. Dr J. Ad. Frahm-Leliveld (1926), Wageningen, Nassauweg 18.
D. Franke, Eernewoude.
R. Frantzen (1922), Rotterdam Z., Leede 22.
Dr A. J. M. Garjeanne (1899), 's-Hertogenbosch, St. Janssingel 19.
Dr S. J. Geerts (1937), Oss, Slachthuislaan 24.
H. van Genderen (1937), Hilversum, Vaartweg 85.
Dr G. Giesberger (1931), Utrecht, Richard Wagnerlaan 22.
Dr W. A. Goddijn (1923), Leiden, Thorbeckestraat 3.
Dr M. A. J. Goedewaagen (1913), Groningen Sterreboschstraat 26.
J. Gombert (1937), Rotterdam, Crooswijkse singel 48.
J. W. Gonggrijp (1941), Amsterdam Z., Schubertstraat 37.
Dr Ir J. A. A. M. Goosens (1933), Wageningen, Rijksstraatweg 59.
Dr A. Gorter (1935), Utrecht, Nieuwe Gracht 199.
Mej. Dr C. J. Gorter (1923), Wageningen, Hamelakkerlaan 20.
G. J. M. A. Gorter (1936), Potchefstroom, Landbouwproefplaas, Transvaal.
Dr A. Grevenstuk (1940), Batavia, Boxlaan 22.
Dr K. Griffioen (1933), Bogor (Indonesia), Dj. Tjikuraj 31.
P. Groenhart (1934), Buitenzorg, 's Lands Plantentuin.
S. Groenhuijzen (1944), Amsterdam, Wijttenbachstraat 14^3.
Dr A. J. Haagen Smit (1932), Pasadena (Calif.), U.S.A., Institute of Technology.
Dr H. de Haan (1922), Wageningen, Prof. Ritzema Bosweg 6.
Dr Iz. de Haan (1928), Wageningen, Meidoornplantsoen 6.
A. J. M. Haans (1947), Utrecht, Choorstraat 14 *bis*.
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Ir E. E. Harmsen (1946,)Boskoop, Goudse Rijweg 82.
Ir M. L. 't Hart (1942), Bennekom, Eekhoornlaan 3.
Mej. Dr A. M. Hartsema (1946), Wageningen, Dr Boeslaan 10.
Dr K. Hartsuijker (1934), Wageningen, Arboretumlaan 9.
H. J. v. Hattum (1947), Leiden, Voldersgracht 5.
J. C. v. d. Have (1949), Groningen, Turftorenstraat 17A.
Mej. S. C. A. Haye (1947), Zeist, Utrechtse weg 10.
Mej. G. R. van Hees (1948), Amsterdam (W.), Paramaribostraat 22II.
Dr R. Hegnauer (1949), Leiden, Pharmaceutisch Laboratorium, Hugo de Grootstraat 32.
Dr J. Heimans, (1912), Amsterdam Z., Leonardostraat 10.
Ir F. Hekker (1944), Delft, Spoorsingel 99.

R. J. Helder (1942), Groningen, Gerbrand Bakkerstraat 83A.
Dr W. F. van Hell (1928), Medan (Deli), A.V.R.O.S.
J. Hendriks (1950), Amsterdam (O), Radioweg 42.
Dr J. Th. Henrard (1912), Oegstgeest, Warmonderweg 54.
Dr A. W. H. van Herk (1926), Amsterdam O., v. d. Waalsstraat 37.
Dr J. W. Hes (1933), Pasoeroean, Java, Proefstation v. d. Java suikerindustrie.
Jhr W. C. van Heurn (1935), Wilp bij Deventer, F 222, Huize „Kleine Noordijk”.
H. M. Heybroek (1949), Wageningen, Oude Bennekomseweg 152.
W. M. Heyl (1920), Oegstgeest, Fred. Hendriklaan 33.
Dr A. N. J. Heyn (1930), Haarlem, Wilhelminapark 13.
T. J. van Heyningen Nanninga (1927), Groningen, Paterswoldseweg 79*a*.
Mej. H. A. Hijink (1950), Utrecht, Mauritsstraat 84.
J. A. Hijner (1947), 's-Gravenhage, Rusthoekstraat 4.
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Mej. Dr K. J. Hocke Hoogenboom (1917), Zonnemaire (Schouwen).
Mej. Dr T. Hof (1931), 's-Gravenhage, Lohengrinstraat 18.
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Mevr. Dr B. A. Honing-Tiddens (1927), Wageningen, Rijksstraatweg 95.
H. Hoogendoorn (1942), Oudewater, Markt B 216.
R. D. Hoogland (1943), Leiden, Haagweg 7*a*.
Dr J. G. ten Houten (1931) Wageningen, Englaan 6.
Dr A. L. Houwink (1928), Delft, Prof. Schoemakerstraat 63.
H. J. Hueck (1945), Leiden, Langebrug 87.
H. S. C. Huijsman (1927), Doetinchem, Ds van Dijkweg 16.
B. Huisinga (1948), Utrecht, Kromme Nieuwe Gracht 28.
Dr F. W. T. Hunger (1895), Voorschoten, Veurse Weg 66.
A. M. Husson S.C.J. (1946), Leiden, St. Jacobsgracht 1.
Mej. E. J. Idenburg (1925), Utrecht, Jan v. Scorelstraat 30 *bis*.
Dr Ir G. van Iterson Jr (1909), Baarn, Eemnesserweg 89.
Mej. W. van Iterson (1938), 's-Gravenhage, Waalsdorperweg 108.
Mevr. F. A. M. Iwema-Veldhuis (1930), Amstelveen, Nieuwenhuysenlaan 2.
J. Izings (1949), Soest, Kolonieweg 6.
Mej. Dr A. Jaarsveld (1930), Amsterdam W., Overtoom 434.
Dr J. C. s'Jacob (1922), Haren (Gr.)., Dilgtweg 28.
M. Jacobs (1950), Leiden, Hoge Woerd 175.
J. A. Janse (1943), Hillegom, Loosterweg III, no 1.
Dr P. Jansen (1902), Amsterdam Z., Frans van Mierisstraat 128.

G. P. J. Jaspers (1945), Gouda, Stoofsteeg 21 (hoek Zeugestr.).
Dr S. C. J. Jochems (1918), Voorst H. 77, post Deventer.
G. J. de Joncheere (1947), Wassenaar, p.a. Jhr. W. E. v. d. Does de Bije, Groot Hoefijzerlaan 61.
B. de Jong (1942), Amsterdam O., Linnaeusparkweg 100^{1}.
Mevr. G. A. de Jonge-Simon Thomas (1950), Naarden, Jan Steenlaan 34.
Dr Ph. de Jongh (1935), Rotterdam, Walenburgenweg 94*b*.
Dr S. E. de Jongh (1932), Leiden, Boerhaavelaan 33.
Dr W. J. Jongmans (1900), Heerlen, Sittarderweg 61.
Dr F. P. Jonker (1932), Utrecht, Zadelstraat 19*bis*.
Mej. Dr A. Kaars Sijpesteyn (1924), Vogelenzang, Vogelenzangseweg 39.
C. Kalkman (1950), 's-Gravenhage, van Diemenstraat 17.
G. A. Kamerbeek (1938), Leiden, Vreewijkstraat 4.
Mej. A. Kamps (1948), Scheemda, Stationsstraat 35B.
Dr W. K. H. Karstens (1931), Leiden, Roodenburgerstraat 18.
Mej. Dr L. C. P. Kerling (1927), Wageningen, Lawickse Allee 7.
J. H. Kern (1937), Bogor, (Indonesia), Kebun Raya.
D. A. Kerpel (1936), Nijmegen, Atjehstraat 71.
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Mej. Dr A. Kleinhoonte (1916), Delft, N. Plantage 13.
Mej. Dr C. H. Klinkenberg (1930), Wageningen, Hamelakkerlaan 3.
E. Kliphuis (1947), Utrecht, Ad. van Ostadelaan 60 *bis*.
Dr Ir A. W. Kloos Jr (1912), Dordrecht, Nieuwe Weg 40.
Ir W. G. van der Kloot (1936), Den Dolder, Taveernelaan 24C.
Dr Ir A. J. Kluyver (1911), Delft, Nieuwe Laan 3.
A. Knol (1927), Baarn, Eemnesserweg 63*a*.
Dr B. Kok (1938), Bilthoven, Beethovenlaan 10.
J. C. N. Kok (1949), Utrecht, Mauritsstraat 68.
Dr V. J. Koningsberger (1917), Utrecht, Nieuwe Gracht 187.
Mej. D. S. F. Kooijman (1945), Maastricht, Koningsplein 111*D*.
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Mej. Dr J. Th. Koster (1925) Oegstgeest, Warmonderweg 48.
Mevr. A. M. Koster-Bouman (1925), Gouda, Crabethstraat 73.
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K. U. Kramer (1950), Bilthoven, Julianalaan 4*A*.
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Mej. A. C. Kreulen (1915), 's-Gravenhage, Schoutenstraat 28.
Dr H. H. Kreutzer (1944), Sittard, Walramstraat 39.
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Dr W. M. Kruseman (1946), Deventer, Sylvanusstraat 11.
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Dr J. Kuijper (1905), Groningen, Troelstralaan 15.
Dr L. W. Kuilman (1928), Buitenzorg, Java, Alg. Proefstation v. d. Landbouw.
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Ch. M. A. Kuyper (1944), Amsterdam Z., Lomanstraat 63.
Dr P. A. v. d. Laan (1929), Buitenzorg, Java, Alg. Proefstation v. d. Landbouw.
Dr Ir J. H. J. van de Laar (1931), Amstenrade, Hommerterweg 43.
Mevr. Dr J. H. H. van de Laar-van der Meer (1917), Amstenrade, Hommerterweg 43.
E. Laarman (1947), Groningen, N. Kijk in 't Jatstr. 82.
J. J. Laarman (1947), 's-Gravenhage, Ampèrestraat 41.
Dr H. J. Lam (1913), Leiden, Rijksherbarium, Nonnensteeg 1.
Dr M. Hille Ris Lambers, Bogor (Indonesia), Fac. van Landbouwwetenschap, van Imhoffplein 1.
Dr J. Lanjouw (1925), Bilthoven, Hercules Seghersslaan 6.
P. Leentvaar (1946), Hilversum, Noodweg 34.
Dr W. C. de Leeuw (1926), Leiden, Roodenburgerstraat 35.
Mej. A. D. Lens (1913), Utrecht, Biltstraat 24 *bis.*
J. C. Lindeman (1946), Utrecht, Lange Nieuwstraat 106.
W. Lindeman (1941), Amsterdam Z., Amstelkade 48 III.
Mej. C. Lingbeek (1950), Utrecht, Prof. Leon Fuchsstraat 18.
Mej. B. A. Lobato (1926), Batavia C., c/o Dept. v. Ond. en Eredienst, Tjilatjapweg.
Mej. Dr J. Lodder (1932), Delft, Nieuwe Plantage 34.
J. C. Lodder (1948), Goes, D. D. van der Boutstraat 4.
W. A. Loeven (1947), 's-Gravenhage, Daguerrestraat 114.
Mej. Dr M. P. Löhnis (1915), Wageningen, Nassauweg 20.
Mej. M. Lucardie (1948), Amsterdam, Beethovenstraat 108 III.
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Mej. W. Manders (1942), Leiden, Boerhaavelaan 12.
Dr A. Manten (1939), Groningen, Florisplein 2*c*.
W. Margadant (1941), Wageningen, Oranjelaan 3.
Mevr. G. W. F. Maris Mc Arthur-Hespe (1937), Amsterdam Z., Herculesstraat 132^{2}.
Dr O. P. Mechelink (1948), Oudenbosch, Markt 34.
Dr A. D. J. Meeuse (1938), 's-Gravenhage, Mispelstraat 11.
Dr B. J. D. Meeuse (1938), Delft, Koornmarkt 24*a*.

J. Meltzer (1941), Bilthoven, Gezichtslaan 60.
Mej. Dr A. M. W. Mennega (1946), Utrecht, Boothstraat 10.
E. A. Mennega (1948), Utrecht, Mariahoek 18.
Mej. Dr M. G. Mes (1934), Afd. Botanie, Universiteit van Pretoria, Transvaal.
G. Meyer (1948), Utrecht, Van Lith de Jeudestraat 13.
W. Meyer (1946), Zaandam, Beethovenstraat 7.
Dr Ir E. Meyer Drees (1935), Bogor (Indonesia), Balai Penjelidikan Kehutanan.
A. Middelhoek (1948), Enschede, Sweelinckstraat 34.
J. A. Miltenburg (1942), Venlo, St. Thomascollege, Hogeweg 22.
A. W. Moll (1934), Amsterdam W., Bonairestraat 15.
Dr J. C. Mooi (1935), Wageningen, Hamelakkerlaan 19.
Dr M F. Mörzer Bruyns (1938), Utrecht, Emmalaan 3.
Dr D. Mulder (1935), Goes, Kloetingseweg 10.
Dr E. G. Mulder (1949), Groningen, Kamplaan 2^1.
F. Muller (1940), Winschoten, Engelse Laan 32.
Dr F. M. Muller (1927), Haren (Gr.), Dilgtweg 30.
J. Muller (1950), Amsterdam (Z), Ruysdaelkade 15^2.
J. R. Müller (1927), Heemstede, Molenlaan 3.
E. T. Nannenga (1930), Heelsum, Doorwerthse straat 4.
J. H. W. Nicolai (1945), Utrecht, Jacob van de Borchstr. 3.
Mej. Dr M. F. E. Nicolai (1929), Leiden, Roodenburgerstraat 16.
Mej. R. van Nie (1946), s'Graveland, Ned. Herv. Pastorie.
Mevr. C. J. Niekerk-Blom (1926), Leiden, Witte Singel 30.
P. J. Nieuwdorp (1938), Leiden, Vreewijkstraat 4.
H. Th. Nieuwenhuijsen (1920), Utrecht, Geertebolwerk 3.
L. E. Nijenhuis (1949), Woerden, Nieuwstr. 17.
R. D. Nijenhuis (1949), Woerden, Nieuwstr. 17.
D. Noordam (1946), Aalsmeer, Kudelstaartseweg 22.
J. Oets (1947), Leonsberg (Suriname), Windhoek 3.
Dr F. J. M. Offerijns (1921), Amsterdam Z., Gerrit v. d. Veenstraat 68.
Mevr. I .Olivier-Luyten (1946), Wageningen, Dr Boeslaan 14.
G. H. Oltheten (1938), Oude Wetering, Kerkstraat 79.
Dr H. C. J. Oomen (1937), Nijmegen, Vossenlaan 53.
P. G. W. J. Oordt Jr, (1949), Utrecht, Wolter Heukelslaan 50.
Dr A. J. P. Oort (1925), Wageningen, Ericalaan 5.
Mej. Dr J. Oortwijn Botjes (1930), Bennekom, Heelsummerweg 11.
M. L. van Oosten (1946), Wageningen, Grindweg 6.
Dr J. Oosterhuis (1921), Zaandam, Westzijde 214.
Dr S. J. van Ooststroom (1927), Oegstgeest, Emmalaan 39.
J. D. Oppenheim (1938), Ramat-Gen (Israel), 26 Hamargoastreet.

Dr W. F. F. Oppenoorth Jr (1932), Delft, Roëllstraat 15.
Dr F. H. L. van Os (1945), Haren (Gr.), Westerse Drift 37.
Dr J. van Overbeek (1930), Modesta (Calif.) U.S.A., Shell Oil Comp.
Dr P. van Oye (1934), Gent, St. Lievenslaan 30, België.
Dr F. van der Paauw (1926), Groningen, Troelstralaan 21*b*.
R. Peelen (1948), Amsterdam, v. Eeghenstr. 111.
Mej. A. J. ter Pelkwijk (1940), Doorn, Koninginneweg 9.
Dr A. C. B. Pfältzer (1922), Twello, Hunderingen.
Dr J. W. Pfältzer (1946), Hilversum, Soestdijkerstraatweg 39.
D. Piet (1946), Amsterdam O., Kruislaan 222.
Dr L. van der Pijl (1926), Zeist, Lommerlust 16.
Mevr. A. J. .v d. Plaats-Niterink (1935), Utrecht, Oudegracht 411.
B. A. de Planque (1947), Utrecht, Weerdsingel W. Z. 62.
D. T. E. van der Ploeg (1940), Akkerwoude (Fr.), Kleine Laan.
Dr J. W. Pont (1921), Pretoria, Bus 994, Z,-Afrika.
Mej. Dr D. J. W. Pool (1919), Groningen, Nassauplein 23*a*.
Dr L. J. Pop (1935), Rolduc, Seminarie.
Mej. A. Post (1949)Groningen, P. Campersingel 231.
Dr W. Postma (1937), Amsterdam Z., Roelof Hartplein 9*hs*.
Dr R. Prakken (1926), Wageningen, Lab. v. Erfelijkheidsonderz. der Landbouwhogeschool.
H. H. Prell (1942), Amsterdam C., Reguliersgracht 12.
Dr W. J. Prud'homme van Reine Jr (1931), Zaandam, Mauvestr.29.
Dr A. A. Pulle (1904), Utrecht, Nachtegaalstraat 28 *bis*.
Dr A. Quispel (1937), Amsterdam, O. Corn. Drebbelstraat 25.
Dr M. H. van Raalte (1928), Wageningen, Bowlespark 25.
A. Récourt (1948), Delft, v. d. Spiegelstraat 27.
H. Reedijk (1946), Gouda, Crabethstraat 45.
Th. J. Reichgelt (1938), Nijmegen, Javastraat 89.
Dr E. Reinders (1923), Wageningen, Nassauweg 5.
Mevr. Dr C. A. Reinders-Gouwentak (1920), Wageningen, Nassauweg 5.
Mevr. R. C. Reinders-Corbach (1947), Wassenaar, Middelweg 6.
Dr J. Reitsma Jr (1926), Buitenzorg, Inst. v. Plantenziekten.
Dr J. F. Reitsma (1913), Rotterdam Nolensstr. 79*a*.
Dr A. F. M. Reynders (1919), Amersfoort, Kapelweg 140.
Dr J. Rietsema (1946), Breda, Brabantlaan 6.
DrJ. R. Rietsema (1946), Wiliamsburg (Mass. U.S.A.) 38 Village Hill.
Mej. C. J. Rijkebusch (1939), Batavia, v. Heutzboulevard 36.
A. H. G. C. Rijven (1946), Utrecht, Poortstraat 38. (vac. Venlo, Roermondsestraat 63).
J. R. Roborgh (1948), Utrecht, Nieuwe Gracht, 26*bis*.

Dr P. A. Roelofsen Jr (1929), Voorburg, Beguinlaan 16.
Ir J. F. Roest (1946), Baarn, Vondellaan 4.
Dr J. W. M. Roodenburg (1919), Utrecht, van Lidth de Jeudestraat 24.
Mej. M. A. J. Rooymans (1948), Amsterdam O., Linnaeushof 66.
P. van Royen (1948), Utrecht, Zadelstraat 38*bis*.
Mej. Dr J. Ruinen (1929), Buitenzorg, 's Lands Plantentuin, Java.
L. de Ruiter (1946), Delft, Delfgauwseweg 190.
Dr J. D. Ruys (1918), Dedemsvaart, Huize De Rollepaal.
G. J. Saaltink (1950), Wageningen, Otto van Gelreweg 13.
A. Salverda (1923), Groningen, C. H. Petersstraat 8.
R. J. Sanders, (1946), Haarlem, Lorentzplein 28.
Mej. M. C. Scherft (1950), Leiden, Rijn en Schiekade 82.
Dr A. Scheygrond (1926), Gouda, Van Itersonlaan 7.
A. Schoenmakers (1930), Bilthoven, Nicolaïlaan 7.
G. Scholten (1949), Maarssen, Zandweg 39.
Mej. H. D. Schotsman (1942), Haren (Gr.), Rijksstraatw. 330.
A. R. Schouten (1947), 's-Gravenhage, van Blankenburgstraat 34.
Mevr. H. W. van Schouwenburg-Mol (1932), Delft, Spoorsingel 83.
Mej. J. C. Schreuder (1933), Groningen, Westerhavenstraat 2^1*a*.
Mej. A. van Schreven (1946), Groningen, Troelstralaan 32*b*.
Dr A. J. Schurink (1935) Soerabaja, Leraar Lyceum, Java.
Dr J. Schweizer (1919), Djember, Java.
G. D. M. Schwencke (1948), Driebergen, „de Horst", Hoofdstr.211.
P. Sevenster (1947), Leiden, W. Singel 61.
C. Sipkes (1917), Rockanje, Rondeweiweg 1.
Dr M. J. Sirks (1911), Groningen, Moddermanlaan 18.
Ir G. Sissingh (1939), Gorssel, Stationslaan G 245.
Jan G. Sloff (1915), Bergen op Zoom, Halsterse Weg E 84.
Dr E. van Slogteren (1912), Lisse.
Ir D. H. M. van Slogteren (1950), Lisse, Laboratorium voor Bloembollenonderzoek.
Mej. W. Slooff (1934), Makassar, Inst. v. Plantenziekten.
Dr D. F. van Slooten (1933), Buitenzorg, Goaweg 88. (Java).
A. Slootweg (1947), Lisse, Hobahostraat 4.
H. R. Smissaert (1950), Leiden, Haarlemmerstraat 200A.
Mej. C. M. L. Smulders (1928), Amsterdam Z., Quinten Massysstraat 18.
Mej. J. C. Sobels (1927), Utrecht, W. Heukelslaan 7.
Ir J. L. van Soest (1920), 's-Gravenhage, van Soutelandelaan 35.
Mej. A. M. H. van Someren (1944), Velp (Gld.,) Dennenweg 3.
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Ir A. M. Sprenger (1918), Wageningen, Lab. v, Tuinb. Plantenteelt, Haagsteeg 3.
Dr C. Spruit P. Pz. (1914), Amsterdam, Eendrachtstraat 12 I.
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Dr J. C. van der Steen (1944), Utrecht, Mauritsstraat 70.
Dr C. C. G. J. van Steenis (1922), Buitenzorg, Java, Kon. Plantentuin van Indonesië.
D. Stegwee (1950), Amsterdam (C), Henri Polaklaan 28.
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C. Steneker (1946), Overveen, Julianalaan 52.
Mej. Th. M. Stienstra (1950), Amsterdam Z., Churchilllaan 292.
A. L. Stoffers (1948), Utrecht, Maliesingel 48*bis*.
A. Stolk (1939), Rotterdam W., G. v. d. Lindestraat 18.
Mej. A. C. Stolk (1937), Baarn, d'Aulnislaan 5.
Dr Th. J. Stomps (1908), Amsterdam C., Plant. Middenlaan 7.
P. Stoutjesdijk (1948), Hollandsche Rading, Spoorlaan 35.
H. J. Swart (1948), Utrecht, Croeselaan 242.
Dr J. J. Swart (1921), Schalkhaar bij Deventer, „de Pieterman," Park Braband.
Dr P. M. L. Tammes (1926), Velp, Hoofdstraat 26.
Mej. W. Terpstra (1948), Utrecht, Willem Barendsstraat 22*bis*.
A. L. Thierens (1938), Wageningen, Nassauweg 30.
Dr J. B. Thomas (1931), Utrecht, Laan van Minsweerd 51.
Dr T. H. Thung, (1946), Wageningen, Lab. v. Mycologie en Aardappelonderzoek, Binnenhaven 4.
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F. Tjallingii (1931), Venlo, Dr Blumenkampstraat 15.
A. J. v. Tooren (1947), Groningen, Sav. Lohmanplein 4B.
Dr H. J. Toxopeus (1923), Wageningen, Nude 66, Inst. Vered. Landb. gew.
P. Triebels (1939), Nijmegen, Sint Annastraat 159.
Mevr. Dr J. Uri (1949), Guayaquil (Ecuador) Casilla 4018.
F. M. van der Vaart (1937), Wageningen, Oranjelaan 20.
Dr K. F. Vaas (1934), Lab. v. d. Binnenvisserij, Buitenzorg, Java.
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Dr R. van der Veen (1927), Eindhoven, Hazeloop 7.
J. H. Venekamp (1950),Haarlem, Joh. de Breukstraat 15.
Dr H. J. Venema (1945), Wageningen, Diedenweg 171.
Mej. C. Venverloo (1950), Leiden, de Sitterlaan 3A.

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Dr W. Vervoort (1939), Leiden, Meezenstraat 1.
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Ir J. Vlieger (1933), Leeuwarden, Fred. Ruyschstraat 6.
A. C. van der Vliet (1922), Rotterdam W., Heemraadsplein 15*b*.
Dr Ir H. van Vloten (1920), Wageningen, Belmontelaan 5.
Mej. M. C. Vreede (1937), Haarlem, Westerhoutpark 36.
Dr D. M. de Vries (1921), Wageningen, Bowlespark 10.
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